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Stochastic Metapopulation Persistence in Heterogeneous Landscapes:
Model-based Contributions to Metapopulation Theory and Conservation Management

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Stochastic Metapopulation Persistence in Heterogeneous Landscapes –

Model-based Contributions to Metapopulation Theory and Conservation Management

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Dedicated to my parents

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Chapter 1

Introduction

1.1 General background

Analyzing environmental problems, developing sustainable solutions, and providing appropriate aids for management support and policy advice: all these tasks are central objectives of environmental research. Undoubtedly, modelling and system analysis are powerful approaches in this field. Models allow environmental effects to be quantified and predicted, the relative importance of factors to be determined, alternative scenarios to be simulated, assessed and ranked according to their effect, and so management prioritizing to be supported. However, there are still some methodological challenges to be mastered:

Firstly, it is neither possible nor useful to start a new research project (e.g. record of empirical data, experiments, model analyses) for each new case study. Therefore, guidelines are needed for solving a certain environmental problem at arbitrary sites. This indicates the urgent need to obtain a comprehensive mechanistic understanding of the factors, processes and interactions driving the environmental problem and to search for general principles and other transferable findings. Hence, generalization and theory building are required. Both, however, are hampered by complexity that is typical for environmental problems. Therefore, special methods of model building and model analysis are needed which support generalization and theory building under complexity.

Secondly, decision-makers can only benefit from the advantages of models if they have access to an implemented version of the model (e.g. in form of computer programs) or to any other tool which allows the same conclusions to be drawn as the original model. Such alternative tools exist (e.g. special indices or rules of thumb). However, a systematic methodology for the derivation of model-based tools for decision-support is missing.

To develop a universal *methodology for using models for theory building and deriving model-based tools for decision-support* is almost impossible. The sources of complexity as well as the demands from theory and management are specific for the environmental problem addressed. Therefore, it is useful to follow an alternative *problem-oriented approach.* The idea is to start with a particular environmental problem, to develop model-based methods for supporting theory building and management in this context, and then to extend what we have learned to other fields. This idea markedly motivated the thesis.

1.2 Subject and aim of the thesis

The thesis addresses the subject of stochastic (1-species) metapopulation persistence in spatially heterogeneous landscapes. A matter of particular interest is the interplay between landscape structure, species' ecology and stochasticity and its effect on metapopulation persistence. The thesis aims at (a) contributing to theory building and management support in this context by the mean of modeling, (b) developing appropriate methods of model building and analysis where necessary, and (c) making the methodological experience gained in the course of the studies applicable to other fields of environmental research.

The concept *"metapopulation"* was introduced by Levins (1969). He defined a metapopulation to be a set of local populations living in isolated habitat islands (so-called patches) with a certain risk of extinction. After local extinction, dispersing individuals can recolonize an empty patch and establish a new population. Hence, recolonization can partly compensate the effect of local extinction and stabilize the overall metapopulation.

To address the subject of metapopulation persistence and to analyze its dependence on landscape structure, species' ecology, and stochasticity is *relevant* in several respects:

1. The interrelation between spatial patterns and ecological processes in general and

between landscape structure and metapopulation persistence in particular are core topics of spatial ecology (e.g. Lefkovitch and Fahrig 1985; Levin 1992; Doak *et al.* 1992; Adler and Nuernberger 1994; Durrett and Levin 1994; Hanski 1994; Day and Possingham 1995; Bascompte and Solé 1998; Frank and Wissel 1998; Hanski and Ovaskainen 2000). Evidently, the essential processes of every metapopulation dynamics (extinction, recolonization) depend on several spatial factors such as patch size, patch distance, number and location of corridors or barriers but also on certain species-ecological attributes such as the species' dispersal range. This indicates that the dynamics and persistence of metapopulations can only be fully understood if the interaction between the different components of the landscape structure (e.g. patch number; patch configuration; patch size distribution; arrangement of corridors/barriers) and the species' ecology are taken into account.

2. In the last few decades, a worldwide loss of species has been reported. Habitat loss and fragmentation belong to the drivers of this environmental problem (e.g. Nee 1994; Moilanen and Hanski 1995; Bascompte and Solé 1996; Fahrig 1997, 2001, 2002; With and King 1999; Wiegand *et al.* 2005). Hence, it is not surprising that both are subject of recent research in population, community and landscape ecology where they are addressed from a theoretical as well as conservational point of view. Emphasis is placed on (a) obtaining a comprehensive mechanistic understanding of the consequences of habitat loss and fragmentation for the structure, dynamics and stability of ecological systems and for species' survival, (b) identifying critical patterns of habitat loss and fragmentation, (c) determining factors which amplify or compensate caused negative effects, and (d) revealing ways of mitigating these effects. A sound understanding of the relationship between landscape structure and metapopulation persistence would contribute to a better understanding of habitat loss and fragmentation and their effects on metapopulations. Moreover, note that stochasticity is always a key factor of species' survival. Thus, it is indispensable to take all relevant sources of stochasticity into account.

3. Evidently, it is urgently needed to develop strategies for both effectively counteract-

> ing the negative effects of habitat loss and fragmentation on species' survival and preventing such impacts from the beginning. A comprehensive understanding of the (landscape-structural and species-ecological) preconditions of metapopulation persistence would strengthen the scientific basis for the development of such strategies. It would indicate under which conditions a certain strategy is actually effective, which species benefit, and how can positive effects be maximized.

All these arguments show that the subject of metapopulation persistence is closely related to recent research questions of both ecological theory and conservation management. Below, we explain in more detail which research questions we want to address:

A lot of modeling work has been done in the context of metapopulations, in the realm of specific case studies as well as more theoretical analyses (for a review, see Ovaskainen and Hanski (2004); cf. references in Chapters 3 to 6). Important effects have been disclosed in this way. However, some snags still exist: Firstly, there are different models in use which vary in the spatial or temporal structure, or in the level of detail. Secondly, in most studies, certain parameters are fixed, just in order to avoid a too high degree of complexity. In the result, however, certain interactions remain unexplored. Evidently, the two effects cause an incomparability of the model results and impede a comprehensive understanding. This hampers generalization and indicates the *need of unification*. The wish to contribute to unification and generalization markedly motivated the work in the thesis. Our *strategy* to meet this objective is based on the following idea: We start with the development of a modeling framework which combines closeness to biological realism with tractability (management of complexity). This modeling framework is later used for all the analyses of metapopulation persistence carried out in the thesis to the benefit of comparability. The decisive feature of the modeling framework is its tractability. It opens the possibility to perform more systematic analyses of the interplay between landscape structure, species' ecology, and stochasticity and its effect on metapopulation persistence. In any case, the results of these analyses contribute a better understanding of metapopulation persistence: they either provide insight into interrelations which have so far not been investigated or they provide information about the robustness of known effects to the choice of models.

Mechanistic understanding of the interplay between landscape structure, species' ecology, and stochasticity and its effect on metapopulation persistence is also a key element of our *strategy to derive model-based tools for decision-support* in metapopulation management. We follow a context-based approach. This means that we start with particular questions of metapopulation management. In the context of these questions, we search for key effects of the landscape structure and analyze their dependence on species' ecology and stochasticity. Finally, we describe the found effects by the mean of simple verbal rules of thumb. These rules can be characterized as "ecologically differentiated" because they address effects of the landscape structure by taking the influence of species' ecology and stochasticity into account. This is progress in view of the fact that most of the existing rules of thumb for landscape management are ecologically neutral. To ignore the species' ecology, however, is a shortcoming because it can lead to counter-productive decisions. In addition to the derivation of (qualitative) ecologically differentiated rules of thumb, we seek for possibilities to derive tools which allow quantitative analyses in the context of the considered question to be supported. In the thesis, we address the following questions of metapopulation management: "What preconditions have to be met to allow long-term metapopulation persistence?", "Which species can benefit at all?", "Which patch configuration / patch size distribution is optimum?", and "When is using the stochastic approach to metapopulation persistence vital to avoid counter-productive conclusions?".

Generalization and unification as well as all the types of management questions addressed above are *also relevant in other fields* of environmental research. Therefore, it is useful to reflect our work in the context of metapopulation persistence (especially regarding generalization/unification and the derivation of model-based tools for decision-support) and to make the attained methodological experience applicable to other fields.

To conclude, the subject of metapopulation persistence is not only worth to be considered from the point of view of ecological theory and conservation management. It is also a useful starting point for contributions to the methodology of using models for theory building and management support in environmental research and for some reflections about the potential and limitations of the suggested problem-oriented approach.

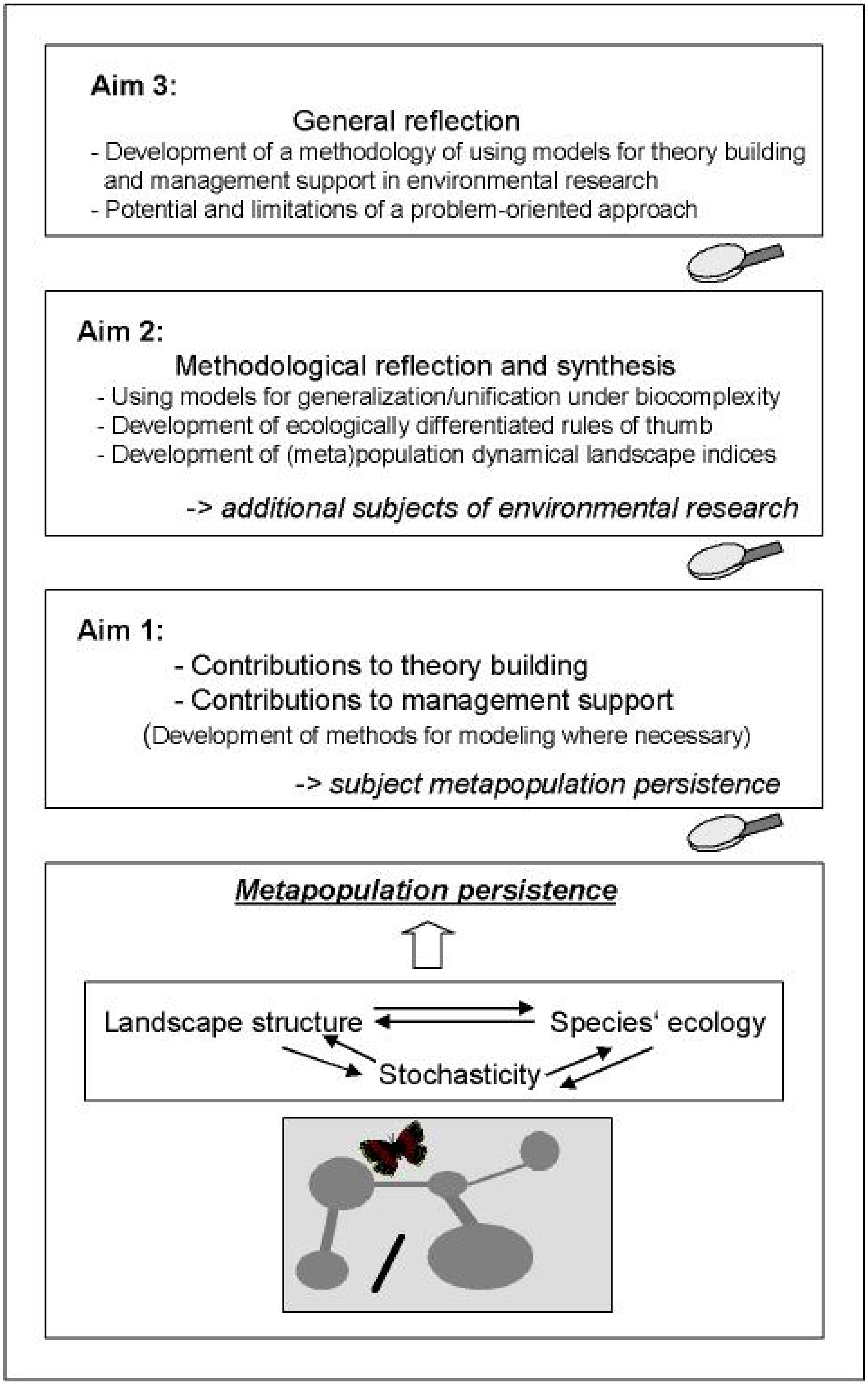

FIGURE 1.1: The conception of the thesis

1.3 Structure of the thesis

The structure of the thesis reflects the dual aim of the thesis (contributions to theory building and management support in the field of metapopulation persistence; methodological development work to the benefit of additional fields). The thesis consists of four parts:

Part I: The modeling framework

Chapter 2: Development of the stochastic modeling framework

Part II: Analyses of metapopulation persistence

Chapter 3: An approximation formula for the mean lifetime T_m

Chapter 4: Minimum conditions for long-term metapopulation persistence

Chapter 5: Optimum patch size distribution

Chapter 6: Unifying stochastic and deterministic metapopulation persistence

Part III: Beyond metapopulation persistence

Chapter 7: Towards generalization and unification under biocomplexity

Chapter 8: Towards ecologically differentiated rules of thumb

Chapter 9: Towards (meta)population dynamical landscape indices

Part IV: Lessons learnt

Chapter 10: The thesis at a glance

Part I (Chapter 2) is dedicated to the development of the modeling framework underlying all the analyses of metapopulation persistence presented in Part II of the thesis. A common modeling framework guarantees comparability between the different studies that is favorable in view of the synthesis and generalization work needed. The chapter starts with a brief introduction into the concept of metapopulations, a derivation of demands on the modeling framework and, the presentation of the modeling approach followed. Emphasis is placed on the development of the actual model system as well as of the measures of stochastic metapopulation persistence used. The chapter finishes with some remarks on the relation of the modeling framework to other metapopulation models.

Part II (Chapters 3 to 6) is dedicated to the analysis of various aspects of stochastic metapopulation persistence with the aim to support theory building and management in this field. This includes the development of methods of model analysis where necessary. In Chapter 3, an approximation formula for the central measure of metapopulation persistence - the mean lifetime T_m - is derived in order to make more structural persistence analyses possible. Chapters 4 and 5 address minimum and optimum conditions for long-term metapopulation persistence and Chapter 6 the interrelation between deterministic and stochastic metapopulation persistence. Various aspects of landscape structure, species' ecology and stochasticity are systematically varied and analyzed in terms of their effect on metapopulation persistence. In all studies, special model-based tools for decision-support are derived which condense the attained scientific results.

Part III (Chapters 7 to 9) has the aim to make the experience gained in the course of the metapopulation studies applicable to other fields of environmental research. Therefore, Chapters 7 to 9 are primarily dedicated to methodological reflection, review and synthesis on the basis of the thesis (Parts I and II) and the literature. The methodological work addresses three topics: (a) the use of models for generalization and unification under biocomplexity, (b) the derivation of ecologically differentiated rules of thumb for landscape management, and (c) the derivation of (meta)population dynamical landscape indices. In each case, some implications of the results for different fields of environmental research and for various interdisciplinary aspects of landscape management are discussed as well.

Part IV (Chapter 10) is dedicated to the presentation of "the thesis at a glance" to allow a better orientation. This includes the description of subject and aim of the thesis, its relevance, the conception of the different studies, and - of course - an overview over the central results of the thesis ("lessons learnt"). The results of the individual studies (Chapters 3 to 9) are thematically grouped to support a better understanding of the overall effects. The chapter finishes with some concluding remarks on the development of a methodology of using models for theory building and management support in environmental research and on the potential and limitations of a problem-oriented approach.

Each Part is provided with a separate introduction explaining background and general conception of the forthcoming studies and their position in the overall scheme of the thesis. It also gives supplementary information (e.g. whether the material is already published).

1.4 References

Adler, F. R., and B. Nuernberger. 1994. Persistence in patchy irregular landscapes. Theoretical Population Biology 45: 41–75

Bascompte, J. and R.V. Solé. 1996. Habitat fragmentation and extinction thresholds in spatially implicit models. Journal of Animal Ecology 65: 465–473

Bascompte, J., and R. V. Solé, eds. 1998. Modeling Spatiotemporal Dynamics in Ecology. Springer-Verlag, Berlin

Day, J. R., and H. P. Possingham. 1995. A stochastic metapopulation model with variability in patch size and position. Theoretical Population Biology 48: 333-360

Doak, D.F., P.C. Marino, and P.M. Kareiva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersing success: Implications for conservation. Theoretical Population Biology 41: 315

Durrett, R., and S. Levin. 1994. Stochastic spatial models: a user's guide to ecological applications. Philosophical Transactions of the Royal Society London B 343: 329–350

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. J. of Wildlife Management 61: 603–610

Fahrig, L. 2001. How much habitat is enough?. Biological Conservation 100: 65–74

Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. Ecological Applications 12: 346–353

Frank, K., and C. Wissel. 1998. Spatial aspects of metapopulation survival: from model results to rules of thumb for landscape management. Landscape Ecology 13: 363-379

Hanski, I. 1994. A practical model of metapopulation dynamics. J. Anim. Ecol. 63: 151–162

Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. Nature 404: 755-758

Lefkovitch, L.P. and Fahrig, L. 1985. Spatial characteristics of habitat patches and population survival. Ecol. Modelling 30: 297–308

Levin, S.A. (1992). The problem of pattern and scale in ecology. Ecology. 73: 1943–1967

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15: 237–240

Moilanen, A., and I. Hanski. 1995. Habitat destruction and coexistence of competitors in a spatially realistic metapopulation model. Journal of Animal Ecology 69: 141–144

Ovaskainen, O. and Hanski, I. 2004. Metapopulation dynamics in highly fragmented landscapes. in I. Hanski, and O. Gaggiotti (eds.) Ecology, Genetics, and Evolution in Metapopulations, Academic Press, 73-103

Nee, S. 1994. How populations persist. Nature 367: 123–124

Wiegand, Th., Revilla, E., and Moloney, K.A. 2005. Effects of habitat loss and fragmentation on population dynamics. Conservation Biology 19: 108–121

With, K. A., and A. W. King. 1999. Extinction thresholds for species in fractal landscapes. Conservation Biology 13: 314–326

Part I

The modeling framework

Chapter 2

The modeling framework

2.1 The concept “metapopulation”

The concept *“metapopulation”* was introduced by Levins (1969). He defined a metapopulation to be a set of local populations living in isolated habitat islands (so-called patches) with a certain risk of extinction. After local extinction, dispersing individuals can recolonize an empty patch and establish a new population. Hence, recolonization can partly compensate the effect of local extinction and stabilize the overall metapopulation.

2.2 Demands on the modeling framework

The aim of this thesis is the analysis of important aspects of (1-species) metapopulation persistence. A matter of particular interest is the interplay between landscape structure, species’ ecology, and stochasticity in this context. Both theory building and conservation management are to be supported. The development of general concepts and strategies, however, requires a comprehensive mechanistic understanding and the disclosure of principles or other general results. This leads to *special demands* on the modeling framework:

Firstly, the model has to be *structurally realistic* in the sense that essential characteristics of the effect of the landscape structure and the species’ ecology on the metapopulation dynamics are correctly reproduced. There are several aspects of the spatial structure of the habitat network underlying any metapopulation which have to be taken into account:

(a) The attributes of the patches such as size, shape, or habitat quality may influence the risk of local extinction, but also the amount of emigrants leaving a patch or the chance of establishing a new local population. (b) The patch configuration in general and the distances between the patches in particular influence the chance of dispersing individuals of successfully reaching a certain patch. They also can have an effect on the likelihood of simultaneous extinction of local populations. This may occur if critical environmental factors fluctuate in a spatially correlated way on a certain spatial scale. (c) The presence of corridors or barriers can alter the chance of recolonization. The final effect of the habitat network on the metapopulation dynamics, however, is determined by two things: the variety of spatial factors relevant and the individuals' specific response to them. The multitude of landscape-structural and species-ecological factors and interactions which are relevant in the context of metapopulations causes a certain degree of model complexity.

Secondly, the model has to take *stochasticity* into account. It is well-known from the viability analysis of the local populations that every sort of stochasticity (e.g. demographic or environmental stochasticity, catastrophes) is a key factor for populations which are vulnerable to extinction (e.g. Goodman 1987; Mangel and Tier 1993; Foley 1994; Wissel *et al.* 1994). On the level of metapopulations, two sorts of stochasticity can be distinguished which are equivalents to demographic and environmental stochasticity on the level of the local populations (Hanski and Gilpin 1991): (a) stochasticity in the sequence of extinction and colonization events, and (b) regional stochasticity. The latter addresses situations where environmental factors fluctuate in a spatially correlated way (such as temperature and rainfall), and affect the dynamics of several local populations in the same manner. This can result in synchronization or even simultaneous extinction of local populations (Hanski 1989; den Boer 1991). There are a few models which take the resulting correlation of the extinction processes into account (e.g. Harrison and Quinn 1989, Gilpin 1990; Ovaskainen 2002). Most of these models deal with spatial homogeneity, i.e. assume a constant degree of correlation ρ. Sometimes, however, the correlation acts over a certain distance and disappears on a larger spatial scale. Akçakaya and Ginzburg (1991) took this effect into consideration and worked with patch-specific, distance-dependent degrees of correlation ρ_{ij}. Their model, however, was only applied to metapopulations with two and three patches. In any case, there is no standard method of incorporating spatial correlation and regional stochasticity in metapopulation models.

Thirdly, the need to obtain a comprehensive mechanistic understanding and to disclose principles requires generalization work. This is only possible if the model is *tractable*.

In the following, we present the *modeling framework* which underlies all the studies in this thesis (Chapters 3 to 6). A common modeling framework ensures comparability between the different studies that is favorable in view of the synthesis and generalization work needed. In order to reconcile structural realism and tractability and to manage the inherent complexity, we follow a *hierarchical approach*. We start with the development of the stochastic *main model* that focuses on the essential processes of every metapopulation dynamics (e.g. extinction, recolonization). Special efforts are invested in the incorporation of the spatial correlation of the extinction processes and the specification of the measures of metapopulation persistence used in this thesis. We continue with the presentation of a collection of *submodels* which allow the landscape structure and the species' ecology to be integrated. The main model and some of the submodels are taken from Frank and Wissel (1998). The other submodels are taken from the literature in order to cover a wide range of ecologically reasonable situations. In addition to the mathematical definition, we give an ecological justification/interpretation of the individual models. This is done in order to support a better understanding of the later model results. We finalize with an important special case, some remarks on the implementation of the spatial correlation, and the relation of the modeling framework to other spatially realistic metapopulation models.

2.3 The main model

We consider finite metapopulations with N patches each being either empty or occupied by a local population. In the following, we develop a continuous time Markov chain model that allows the main processes of metapopulation dynamics to be described in a patch-specific way. This is a precondition for integrating the effects of the landscape structure at a later stage. As is known from Markov theory (Keilson 1979), such models are determined by (a) the state space, and (b) the matrix of short-term transition probabilities.

2.3.1 The state space

The individual patches i of the metapopulation are assumed to be either empty ($x_i = 0$) or occupied by a local population ($x_i = 1$). The state of the overall metapopulation is described by the vector $\mathbf{x} = (x_1, ..., x_N)$ of the occupancy states x_i of its patches. Evidently, 2^N metapopulation states $\mathbf{x}$ can be distinguished.

2.3.2 The short-term transition probabilities

The main model aims at taking all those processes into account which are essential for every metapopulation. These are obviously extinction and recolonization of patches. However, regional stochasticity (Moran 1953; Ranta et al. 1995; Haydon and Steen 1997) as well as dispersal (Holmes et al. 1994; Bascompte and Solé 1998; Kendall et al. 2000) can synchronize the dynamics within the individual patches. In consequence, several populations can go extinct simultaneously. Therefore, it is useful to distinguish two kinds of extinction: (a) local extinction of single populations caused by certain local drivers, and (b) correlated extinction of several populations caused by certain regional drivers.

In the following, we assume that changes in the metapopulation states $\mathbf{x}$ can only be the result of local extinction, correlated extinction or recolonization. Within a very short time interval Δt, at most one of these processes can occur. The processes themselves are described by the corresponding short-term transition probabilities defined as follows:

1. *Short-term probabilities of local extinction* $w_-(i, \Delta t)$

   A currently occupied patch i goes extinct within a time Δt with a short-term probability $w_-(i, \Delta t) = \nu_i \cdot \Delta t$. The related quantity, $T_i = \frac{\Delta t}{w_-(i,\Delta t)} = \frac{1}{\nu_i}$, is nothing else than the mean lifetime of local population i measured in units of Δt.

2. *Short-term probabilities of correlated extinction* $w_-(i, j, \Delta t)$

   Whenever two patches i and j are currently occupied, they have some chance of simultaneously going extinct within time Δt. If the corresponding local extinction processes are uncorrelated then a simultaneous extinction occurs with the product of the single short-term probabilities $w_-(i, \Delta t) \cdot w_-(j, \Delta t) = \nu_i \, \nu_j \cdot (\Delta t)^2$ that is close to zero. If both extinction processes are completely correlated then simultaneous extinction occurs with a short-term probability $w_-(i,j,\Delta t) = \sqrt{w_-(i,\Delta t)}\sqrt{w_-(j,\Delta t)}$ given by the geometric mean of the local quantities. Hence, in the general case, $w_-(i,j,\Delta t)$ is given by $\rho_{ij} \cdot \sqrt{\nu_i}\sqrt{\nu_j} \cdot \Delta t$ with ρ_{ij} being the actual degree of correlation between the local extinction processes within patch i and patch j.

3. *The short-term probabilities of recolonization* $w_+(i,\Delta t)$

   A currently empty patch i can be recolonized within time Δt by individuals of all patches currently occupied. If $c_{ji} \cdot \Delta t$ denotes the short-term probability that patch i is colonized from patch j then the total short-term probability of recolonization $w_+(i,\Delta t)$ equals the sum $\sum_{x_j=1} c_{ji} \cdot \Delta t$ taken over all patches j currently occupied.

The three kinds of short-term transition probabilities determine the dynamics of the metapopulation. They are completely expressed in terms of three kinds of parameters: the local extinction rates ν_i, the colonization rates c_{ij}, and the degrees of correlation ρ_{ij}.

2.3.3 Implementation of the transition matrix

The "heart" of any Markov chain model is the transition matrix $A = (a_{kn})$. Determining the transition matrix, however, requires that all the states are numbered and changes are described as transitions between state numbers. Then the matrix entries a_{kn} result from the short-term probabilities $a_{kn} \cdot \Delta t$ that state n goes over to state k within a time Δt.

In order to find a suitable rule for numbering in our case, every metapopulation state $\mathbf{x} = (x_1, .., x_N)$ is interpreted as binary code of a certain integer between 0 and $2^N - 1$. Then the state number $n(\mathbf{x})$ belonging to a certain metapopulation state $\mathbf{x}$ is given by

$$n(\mathbf{x}) = \sum_{i=1}^{N} x_i \cdot 2^{i-1}. \tag{2.1}$$

Following this rule, state $\mathbf{x} = (1,0,1,0,1)$ gets state number $n(\mathbf{x})$=1+4+16=21. On the other hand, every integer n can be uniquely expressed as a binary code $\mathbf{x}(n)$ that can be determined by repeatedly applying the following rules:

$$\mathbf{x}(n)_1 = \begin{cases} 0 & \text{for n even} \\ 1 & \text{for n odd} \end{cases} \tag{2.2}$$

$$\mathbf{x}(n)_i = \begin{cases} 0 \\ 1 \end{cases} \text{for } \frac{1}{2^{i-1}} \cdot (n - \sum_{k=1}^{i-1} \mathbf{x}(n)_k \cdot 2^{k-1}) \quad \begin{matrix} \text{even} \\ \text{odd} \end{matrix} \qquad \text{for all i>1}$$

Due to these rules, the integer 11 stands for the state (1,1,0,1,0). The two procedures (2.1) and (2.2) enable us to calculate the number $n(\mathbf{x})$ of a given metapopulation state $\mathbf{x}$, but also to reconstruct the metapopulation state $\mathbf{x}(n)$ that belongs to a given number n. Now the basis is provided for determining the transition matrix $A = (a_{kn})$ for the "state number dynamics" which are given by the short-term probabilities $a_{kn}\Delta t$ that the metapopulation goes over from state number n to state number k within time Δt.

As a basis, we have to reveal how a change in a certain metapopulation state $\mathbf{x}$ is reflected in a change in the corresponding state number $n(\mathbf{x})$. Relation (2.1) shows that any transition of a certain component x_i from 1 to 0 (or from 0 to 1) results in a transition of the state number from $n(\mathbf{x})$ to $n(\mathbf{x}) - 2^{i-1}$ (or from $n(\mathbf{x})$ to $n(\mathbf{x}) + 2^{i-1}$). What changes are permissible depends on $\mathbf{x}$ and the sets of its 1- and its 0-positions defined by

$$I(\mathbf{x}) = \{i : x_i = 1\} \quad , \quad J(\mathbf{x}) = \{j : x_j = 0\}. \tag{2.3}$$

Table 2.I shows the complete list of all permissible $\mathbf{x}$- and $n(\mathbf{x})$-transitions whose probabilities are well-known (Sec. 2.1.2). This enables us to give an algorithm for determining all permissible successors k of a certain integer n together with the matrix entries a_{kn}.

1. Determine $\mathbf{x}(n)$ by using (2.2)
2. Determine $I(\mathbf{x}(n))$ and $J(\mathbf{x}(n))$ by using (2.3).
3. Determine a_{kn} by applying the scheme in Tab. 2.I to the state $\mathbf{x}(n)$:
    - For all $i \in I(\mathbf{x}(n))$: $a_{n-2^{i-1},n} = \frac{w_-(i,\Delta t)}{\Delta t} = \nu_i$
    - For all $i, j \in I(\mathbf{x}(n))$: $a_{n-2^{i-1}-2^{j-1},n} = \frac{w_-(i,j,\Delta t)}{\Delta t} = \rho_{ij}\sqrt{\nu_i}\sqrt{\nu_j}$
    - For all $j \in J(\mathbf{x}(n))$: $a_{n+2^{j-1},n} = \frac{w_+(j,\Delta t)}{\Delta t} = \sum_{i \in I(\mathbf{x}(n))} c_{ij}$
    - For all other $k (\neq n)$: $a_{kn} = 0$

4. All diagonal entries of a transition matrix A meet $a_{nn} = -\sum_{k(\neq n)} a_{kn}$ so that
   - $a_{nn} = -(\sum_{i\in I(\mathbf{x}(n))} \nu_i + \sum_{i,j\in I(\mathbf{x}(n))} \rho_{ij}\sqrt{\nu_i}\sqrt{\nu_j} + \sum_{j\in J(\mathbf{x}(n))} \sum_{i\in I(\mathbf{x}(n))} c_{ij})$

By applying this algorithm to all integers between 0 and $2^N - 1$, the transition matrix $A = (a_{kn})$ can be derived. This matrix summarizes all model parameters $(\nu_i, c_{ij}, \rho_{ij})$ and may be interpreted as a (patch-specific) generalization of the transition matrix of an usual birth and death process (Nisbet and Gurney 1982; Goodman 1987; Wissel *et al.* 1994). Instead of transitions $(n \to n \pm 1)$ we get transitions $(n \to n \pm 2^{i-1})$ for certain integers i.

2.3.4 The dynamic equation and its solution

Due to Markov chain theory (e.g. Keilson 1979), the state number dynamics of every metapopulation are given by the following system of linear differential equations

$$\frac{dP_{nn_0}(t)}{dt} = \sum_{l=0}^{2^N-1} a_{nl} \cdot P_{ln_0}(t) \qquad \text{for all } n_0, n \in \{0, ..., 2^N - 1\}, \tag{2.4}$$

where $P_{nn_0}(t)$ is the probability that the metapopulation which is initially in state n_0 is in state n at time t and $A = (a_{nl})$ is the transition matrix derived by the algorithm described above (Sec. 2.1.3). As is well-known from Markov theory (Keilson 1979, Wissel and Stöcker 1991), system (2.4) can be analytically solved as follows:

$$P_{nn_0}(t) = \sum_{i=1}^{2^N} r_n^i \cdot l_{n_0}^i \cdot e^{\omega_i \cdot t} \qquad \text{for all } n_0, n \in \{0, ..., 2^N - 1\}, \tag{2.5}$$

where ω_i is the i-th eigenvalue, and $\mathbf{l}^i = (l_0^i, ..., l_{2^N-1}^i)$ and $\mathbf{r}^i = (r_0^i, ..., r_{2^N-1}^i)$ the corresponding left and right eigenvectors of transition matrix A. Since $(0, .., 0)$ is an absorbing state, we have $\omega_1 = 0$, $\mathbf{l^1} = (1, 1.., 1)$, and $\mathbf{r^1} = (1, 0, .., 0)$. All the other left and right eigenvectors, $\mathbf{l}^i$ and $\mathbf{r}^i$, are normalized in such a way that $\sum_{j>0} r_j^i = 1$ and $\sum_j r_j^i \cdot l_j^i = 1$. These algebraic terms, $\{\omega_i, \mathbf{l}^i, \mathbf{r}^i\}$, summarize all the effects of the main model parameters $(\nu_k, c_{kj}, \rho_{kj})$ which are relevant for the dynamic behavior of the entire metapopulation.

The actual probabilities of interest $P_{\mathbf{x}\,\mathbf{x_0}}(t)$ that the metapopulation goes over from its initial state $\mathbf{x_0}$ to a certain state $\mathbf{x}$ in time t are given by $P_{n(\mathbf{x})\,n(\mathbf{x_0})}(t)$. These quantities describe the stochastic development of the metapopulation in the course of time.

Table 2.I

The complete list of all state transitions permissible for a given metapopulation state $\mathbf{x} = (x_1, .., x_N)$. For the definition of $n(\mathbf{x})$ see (2.1), for those of $I(\mathbf{x})$ and $J(\mathbf{x})$ see (2.3).

Process	$\mathbf{x}$–transition	$n(\mathbf{x})$ – transition
Local extinction $i \in I(\mathbf{x})$	$(.., \underset{i}{1}, ..) \rightarrow (.., \underset{i}{0}, ..)$	$\mathrm{n}(\mathbf{x}) \rightarrow n(\mathbf{x}) - 2^{i-1}$
Correlated extinction $i, j \in I(\mathbf{x})$	$(.., \underset{i}{1}, .., \underset{j}{1}, ..) \rightarrow (.., \underset{i}{0}, .., \underset{j}{0}, ..)$	$n(\mathbf{x}) \rightarrow n(\mathbf{x}) - 2^{i-1} - 2^{j-1}$
Recolonization $j \in J(\mathbf{x})$	$(.., \underset{j}{0}, ..) \rightarrow (.., \underset{j}{1}, ..)$	$n(\mathbf{x}) \rightarrow n(\mathbf{x}) + 2^{j-1}$
Nothing occurs	$(x_1, .., x_N) \rightarrow (x_1, .., x_N)$	$n(\mathbf{x}) \rightarrow n(\mathbf{x})$

2.3.5 Quasi-stationarity and metapopulation persistence

A quantity of particular importance in connection with metapopulation persistence is the survival chance $S_{\mathbf{x_0}}(t)$, i.e. the probability that a metapopulation with initial state $\mathbf{x_0}$ is not extinct at time t. Evidently, $S_{\mathbf{x_0}}(t) = \sum_{\mathbf{x} \neq (0,..,0)} P_{\mathbf{x}\mathbf{x_0}}(t) = \sum_{n>0} P_{nn(\mathbf{x_0})}(t)$. The functional structure of $S_{\mathbf{x_0}}(t)$ can be further specified:

$$\begin{aligned} S_{\mathbf{x_0}}(t) = \sum_{n>0} P_{nn(\mathbf{x_0})}(t) &= \underbrace{(\sum_{n>0} r_n^1)}_{=0} \cdot l^1_{n(\mathbf{x_0})} \cdot e^{\omega_1 \cdot t} + \sum_{i=2}^{2^N} \underbrace{(\sum_{n>0} r_n^i)}_{=1} \cdot l^i_{n(\mathbf{x_0})} \cdot e^{\omega_i \cdot t} \\ &= \sum_{i=2}^{2^N} l^i_{n(\mathbf{x_0})} \cdot e^{\omega_i \cdot t}. \end{aligned} \tag{2.6}$$

Moreover, it is well-known that Markov chain models show a typical dynamic behavior in most cases (e.g. Darroch and Senata 1965; Keilson 1979; Wissel and Stöcker 1991; Pollett 1997; Grimm and Wissel 2004): If the metapopulation is initially in state $\mathbf{x_0}$ then a certain percentage of the runs indicates rapid extinction, while the remaining runs indicate rapid approach to *quasi-stationarity*. Quasi-stationarity means that the metapopulation shows typical fluctuations in the occupancy patterns before extinction, while extinction occurs with a constant probability per time. Mathematically spoken, the short transition phase mentioned is equivalent to the condition $\omega_3 << \omega_2$. Then relation (2.6) indicates that

$$S_{\mathbf{x_0}}(t) \approx c_{\mathbf{x_0}} \cdot e^{-t/T_m} \quad \text{with} \quad c_{\mathbf{x_0}} := l^2_{n(\mathbf{x_0})} \text{ and } T_m := -1/\omega_2 \tag{2.7}$$

for larger values of t. Evidently, the survival chance of a metapopulation with initial state $\mathbf{x_0}$ at time t is determined by two quantities: $c_{\mathbf{x_0}}$ and e^{-t/T_m}. The term $c_{\mathbf{x_0}}$ is the probability that the metapopulation successfully approaches quasi-stationarity. It summarizes all the effects of the initial state $\mathbf{x_0}$ relevant for persistence. The term $S^*(t) := e^{-t/T_m}$ is the survival chance of the metapopulation after reaching quasi-stationarity. It is completely determined by T_m, the mean lifetime of the (quasi-stationary) metapopulation. T_m is given by the reciprocal value $-1/\omega_2$ of the mentioned rate of metapopulation extinction, $-\omega_2$. It summarizes all the effects of the quasi-stationary phase of the metapopulation dynamics relevant for persistence. T_m is independent of the initial state $\mathbf{x_0}$. Both $c_{\mathbf{x_0}} = l^2_{n(\mathbf{x_0})}$ and $T_m = -1/\omega_2$ can be determined by eigensystem analysis of the transition matrix A.

Relation (2.7) has an important implication. If quasi-stationary metapopulations are considered (as is done in Chapters 3 to 5) then the mean lifetime T_m provides an adequate measure of metapopulation persistence. In all other cases, the initial states have to be included in the persistence analysis (via $c_{\mathbf{x_0}}$) as well. One major advantage of relation (2.7) is that it allows us to distinguish between initial and quasi-stationary effects on (stochastic) metapopulation persistence (see also Grimm and Wissel (2004)).

2.3.6 Some remarks on the main model

The presented main model belongs to the class of Levins-type (synonymously winking / presence-absence / patch occupancy / 0-1-) models which are widely used in the field of metapopulation modeling (e.g. Quinn and Hastings 1987; Verboom et al. 1991; Hanski 1994). These models do not explicitly take within-patch dynamics into account. But according to Drechsler and Wissel (1997), this is actually unnecessary in most cases (except under extremely strong environmental fluctuations), at least as long Allee or rescue effects are of no bearing. All the effects of the local factors (including population size) with relevance for metapopulation persistence are summarized and implicitly included in the parameters describing the resulting patch dynamics, i.e. the changes between "occupied" and "empty" (here: ν_i, c_{ij}, ρ_{ij}). For a more detailed discussion of the chances and limitations of separating local and regional dynamics, see Chapter 7 (Section 7.2.1)

Because of its implementation as a continuous time, finite Markov chain, the main model reflects the discreteness of the patches and takes the stochasticity in the sequence of extinction and colonization events into account. The way in which this sort of metapopulation stochasticity is modeled is consistent with the "birth and death process"-based implementation of demographic stochasticity (e.g. Goel and Richter-Dyn 1974; Goodman 1987; Wissel *et al.* 1994) on the level of the dynamics of single population.

The main model is patch-specific, i.e. the complete occupancy vector $\underline{x} = (x_1, ..., x_N)$ is used to describe the metapopulation dynamics, instead of the number n or the percentage p of occupied patches as is done by the classical metapopulation models (e.g. Levins 1969, Nisbet and Gurney 1982). All the relevant process parameters (e.g. ν_i, ρ_{ij}, c_{ij}) are patch-specific as well. This allows us to distinguish between the individual patches, that is the precondition for integrating landscape structure and species' ecology.

2.4 The submodels to integrate landscape structure and species ecology

So far, we exclusively discussed about the main model that merely focuses on the main processes of metapopulation dynamics (local extinction, correlated extinction, colonization). In the following, we present submodels which allow the main model parameters (ν_i, ρ_{ij}, c_{ij}) to be linked to the relevant spatial aspects of the habitat network underlying the metapopulation and the species' response to them. But as required in the context of the main model, the submodels have to be as simple as possible too, in order to support generalization work. As a pre-condition, each parameter has to be analyzed in terms of what aspects of the spatial structure of the habitat network are typically relevant.

As was already mentioned, the spatial structure of the habitat network underlying a metapopulation is characterized by various factors such as the number, size, shape and habitat quality of the patches, the configuration of the patches, and - if relevant - the number and relative arrangement of corridors or barriers. In order to avoid an overloading of the studies in this thesis with too many spatial effects, we make the following simplifying assumptions: (a) all patches have *circular shapes*; (b) all patches have the *same habitat quality*; (c) the distance d_{ij} between two patches i and j is measured from *centre-to-centre*.

2.4.1 A submodel for the local extinction rate ν_i

According to numerous stochastic population models (e.g. Goel and Richter-Dyn 1974; Goodman 1987; Lande 1993; Foley 1994; Wissel et al. 1994; Wissel and Zaschke 1994), the extinction rate ν_i of the local population in patch i depends on the carrying capacity K_i and so the size A_i of patch i. The smaller the patch, the higher the risk of local extinction. Many models show a power-like relationship between ν_i and A_i, i.e.

$$\nu_i = \epsilon \cdot A_i^{-x}, \tag{2.8}$$

where ϵ and x are two species-specific parameters. The power x strongly depends on the strength of environmental noise in the local populations which summarizes both the strength of the relevant environmental fluctuations and the species' response to them. The stronger the environmental noise, the smaller the value of x. The extinction parameter ϵ summarizes all the other demographic details relevant for local extinction. Relation (2.8) is used as standard submodel for the local extinction rate ν_i in this thesis.

Usually, both x and ϵ depend on habitat quality and are therefore species- and patch-specific. In this study, however, we assume that all the patches have the same quality, just in order to avoid an overloading with too many spatial aspects in the first step. In consequence, x and ϵ can assumed to be constant, i.e. independent of the patch numbers i.

Submodel (2.8) indicates that the local extinction rate ν_i is completely determined by the local (within-patch) settings and independent of all other patches. This implicitly assumes that *rescue effects* (Brown and Kodric-Brown 1977) are of no bearing. Note that this is equivalent to the simultaneous occurrence of the following two conditions: (a) dispersal is such strong that the metapopulation reaches quasi-stationarity, and (b) dispersal does not affect the risk of local extinction through its effect on the population size.

2.4.2 A submodel for the degree of correlation ρ_{ij}

The degree of correlation ρ_{ij} of the extinction processes (Hanski 1989; Harrison and Quinn 1989; Gilpin 1990) may decrease with the distance d_{ij} between the patches (Baars and van Dijk 1984; Hanski and Woiwod 1993; Myers and Rothman 1995; Steen et al. 1996; Sutcliffe *et al.* 1996; Ranta et al. 1997; Moilanen *et al.* 1998; Bjørnstad et al. 1999). In order to incorporate this effect in a simple way, we assume an exponential decline that has also been found in nature (Moloney 1993; Akçakaya and Atwood 1997) such that

$$\rho_{ij} = e^{-d_{ij}/d_\rho} \tag{2.9}$$

(Akçakaya and Ginzburg 1991; Frank and Wissel 1998; Frank et al. 2003), where d_ρ is the correlation length, i.e. the mean distance over which the correlation acts. The description of ρ_{ij} as a negative exponential function of d_{ij} ensures that the matrix of the ρ_{ij}-values is positive definite (Burgman et al. 1993), as is required for correlation matrices. Relation (2.9) provides the most simple submodel that allows us to incorporate spatial aspects of the correlation of extinction and to analyze their effects on the metapopulation dynamics at all. However, one also should have in mind that the submodel only covers a particular but important range of situations, as the following arguments indicate:

Firstly, the submodel implicitly assumes that the critical, synchronizing environmental factors are located in the patches themselves and radiate into the neighborhood in a concentric, distance-dependent way. This is the case if extinction is caused by the invasion of predators or the spread of a disease. The assumption is also valid if dispersal synchronizes the dynamics of the local populations as is known from several theoretical studies (Holmes et al. 1994; Bascompte and Solé 1998; Kendall et al. 2000).

Secondly, the submodel is not valid anymore if extinction is caused by hazards with a fixed or randomly varying origin. In this case, the degree of correlation ρ_{ij} of the extinction processes does not depend on the distance d_{ij} between the patches i and j but on the distances $d_{i,H}$ and $d_{j,H}$ to the origin of the hazard, H. For this situation, Ovaskainen (2002) developed an alternative, algorithmic submodel for the correlation.

Thirdly, the distance between the patches is not the only spatial factor that may influence the correlation of extinction. Different micro-climatic conditions due to different topographic exposures of the individual patches (e.g., north or south slope), for instance, can asynchronize the within-patch dynamics even if the relevant environmental factors (e.g., temperature or moisture) fluctuate in a correlated way. Such habitat-quality-induced asynchronization effects are known for insect populations (e.g., Harrison *et al.* 1988) but also for populations of small mammals (e.g. Grimm *et al.* 2003). Unfortunately, there are no standard models describing the functional relationship between habitat quality pattern and the resulting correlation of extinction.

2.4.3 A submodel for the colonization rate c_{ij}

A successful colonization of a certain patch is the result of different local and regional processes: (a) emigration from a certain start patch, (b) dispersal through the landscape, and (c) immigration and establishment of a new local population in the target patch. Therefore, the colonization rate c_{ij} can be subdivided into a local and a regional part, i.e.

$$c_{ij} = \gamma \cdot E_i \cdot a_{ij}, \tag{2.10}$$

where E_i is the mean number of emigrants leaving the local population in patch i per time and a_{ij} the arrival probability, i.e. the probability of a disperser from patch i successfully reaching patch j. If Δt denotes a short time-interval then the product $E_i \cdot a_{ij} \cdot \Delta t$ gives the mean number of dispersers of patch i immigrating into patch j within time Δt. How successful these immigrants are depends on the parameter γ. It denotes the probability that a single immigrant initiates a successful establishment. This parameter is “adopted” from Island Theory (MacArthur and Wilson 1967). In this theory, the probability $p_e(I)$ that I immigrants successfully establish a new population in an empty patch is described by $p_e(I) = 1 - e^{-\gamma \cdot I}$. By inserting the number of immigrants $I = E_i \cdot a_{ij} \cdot \Delta t$ into this function, we get $p_e(E_i \cdot a_{ij} \cdot \Delta t) = 1 - e^{-\gamma \cdot E_i \cdot a_{ij} \cdot \Delta t} \approx \gamma \cdot E_i \cdot a_{ij} \cdot \Delta t$, as long as Δt is small enough. The overall colonization rate c_{ij} results from $c_{ij} = \frac{p_e(E_i \cdot a_{ij} \cdot \Delta t)}{\Delta t} = \gamma \cdot E_i \cdot a_{ij}$.

2.4.3.1 The number of emigrants E_i

The local part of colonization rate c_{ij}, i.e. the mean number of emigrants E_i leaving patch i per time, is related to the mean population size and, hence, to the area size A_i of the patch. We assume a power-like relationship between E_i and A_i, i.e.

$$E_i = \delta \cdot {A_i}^b. \tag{2.11}$$

This approach is flexible enough to cover both density-independent emigration where a certain proportion of the population leaves the patch ($b = 1$) and situations where individuals at the edge of the patch have a higher probability of leaving than individuals in the core. For a wide range of inner-habitat movement, $b = 0.5$ has been found to be a good estimate, as is indicated by Moilanen's Virtual Migration Model (Hanski *et al.* 2000). The parameter δ can be interpreted as species-specific emigration parameter.

2.4.3.2 The arrival probability a_{ij}

The regional part of c_{ij}, i.e. the arrival probability a_{ij}, usually depends on several factors: the patch configuration, the structure of the matrix between the patches, and the species' dispersal strategy. It makes difference whether the individuals are passively dispersed (e.g. by wind) or actively move through the landscape. Since we are interested in obtaining a comprehensive mechanistic understanding of the role of landscape structure and dispersal behavior and dispersal is always a crucial process in spatial population ecology, we do not provide only one particular submodel for the arrival probability a_{ij}. In order to cover a wide range of ecologically reasonable situations, we provide two submodels for "passive dispersal" and two submodels for "active dispersal", each widely used in literature.

Passive dispersal (The "Simple exponential model")
In this case, the dispersers are assumed to be transported by a certain medium (e.g. wind). In consequence, the transport behavior of the medium determines the position of the dispersers at a given time. The most simple transport model assumes a 1-dimensional diffusion towards patch j with a constant rate with which the emigrants settle down. In this case, the probability of arrival a_{ij} coincides with the probability that the final position of the disperser is inside patch j. As is well-known from diffusion theory, this probability is given by a negative exponential function of the distance d_{ij}, i.e.

$$a_{ij} = e^{-d_{ij}/d_a} \tag{2.12}$$

(see also equation (6.4) in Turchin (1998)), where d_a is the mean distance from release point at which the dispersers settle down. In this study, this parameter is referred to as "mean dispersal range". Although a 1-dimensional diffusion model seems to be unrealistic for describing dispersal processes in a (2-dimensional) landscape, the simple negative exponential function has been found to be able to appropriately fit dispersal data of large number of species (Wolfenbarger 1946). This is certainly the main reason why this model is so extensively used (e.g., Fahrig 1992; Hanski 1994; Adler and Nuernberger 1994; Vos et al. 2001) for incorporating the effect of dispersal in metapopulation models.

Passive dispersal (The "Pie-slice model")

A more realistic transport model is the so-called "Pie slice model" (e.g. Etienne and Heesterbeek 2000) that assumes a 2-dimensional diffusion with a constant rate of settling down. This model takes into account that a single disperser only successfully arrives at a certain patch if it is transported over the correct distance, but also in the correct direction. The directionality effect is incorporated in the following manner: Transport of dispersers starts in the centre of patch i. Then all those directions are defined to be suitable which lie in the segment of a circle of radius d_{ij} around patch i that is determined by the two tangents to patch j. The portion of suitable directions is therefore given by the relative size of this segment measured as portion of the size of the whole circle. The size of the segment coincides with the diameter D_j of patch j that is given by $\frac{2\cdot\sqrt{A_j}}{\pi^{1/2}}$. To see this, remember that all patches are assumed to have circular shapes. In this case, there is a clear relationship between diameter D and area A, namely $D = \frac{2\cdot\sqrt{A}}{\pi^{1/2}}$. The perimeter of the whole circle is given by $2\pi d_{ij}$. Hence, the portion of suitable directions can be approximated by the ratio $(\frac{2\cdot\sqrt{A_j}}{\pi^{1/2}})/(2\pi d_{ij})$. The final arrival probability a_{ij} results from multiplying this portion with the probability of settling down at distance d_{ij}. Hence,

$$a_{ij} = \frac{\sqrt{A_j}}{\pi^{3/2}} \cdot \frac{1}{d_{ij}} \cdot e^{-d_{ij}/d_a}. \tag{2.13}$$

In this case, the arrival probability a_{ij} depends on both the distance d_{ij} between the patches i and j as in the simple exponential model (2.12) and on the size A_j of patch j.

Active dispersal (The "Corridor-attraction model")

So far, we considered situations where the dispersers are transported by a certain medium.

Now we shift the focus of attention to situations where the dispersers actively move through the landscape. In this case, the individuals make decisions concerning where to go or whether to stay or not. Frequently, they respond to certain landscape elements which effectively "guide" the individuals through the landscape. We start with a situation where some patches in the habitat network are connected by corridors and where the dispersers respond to the corridors which are adjacent to their start patch i. We assume that all the corridors have the same attractiveness. In this case, each disperser randomly chooses one of the n_i adjacent corridors. Since the probability that it really reaches the patch j at the other end of the corridor is given by e^{-d_{ij}/d_a}, we obtain

$$a_{ij} = \begin{cases} \frac{1}{n_i} \cdot e^{-d_{ij}/d_a} & \text{if } i \text{ and } j \text{ are connected by a corridor} \\ 0 & \text{else} \end{cases} \tag{2.14}$$

(e.g. Henein and Merriam 1990; Frank 1998, 2004; Frank et al. 2003). Evidently, the arrival probability a_{ij} depends on several spatial factors: the distance d_{ij} between patches i and j, the presence of a corridor between these two patches, and the total number of corridors n_i adjacent to patch i. Hence, the arrival probability a_{ij} can only be correctly specified if the entire pattern of connectedness (number and relative arrangement of corridors) in the habitat network is taken into account. In the *special case* of *complete connectedness* (all patches are connected with each other by a corridor), we get the following simplified submodel:

$$a_{ij} = \frac{1}{N-1} \cdot e^{-d_{ij}/d_a} \tag{2.15}$$

(Frank and Wissel 1998, 2002). The assumption of complete connectedness is certainly unrealistic in most situations and rather hypothetical. Nevertheless it provides an important reference case for analyzing the effect of active movement in patchy landscapes.

Active dispersal (The "Patch-attraction model")

Now we consider a completely different situations: patchy landscapes without any corridors or barriers but spatially homogeneous matrix habitat between the patches. The dispersers are assumed to move through the landscape according to random and more systematic rules. Additionally, they are assumed to be able to perceive patches within a certain critical distance (perceptual range; see e.g. Zollner and Lima (1999); Conradt et al. (2000); Heinz et al. (2004) and references therein), to go straight to a patch perceived and to stay there. Such a situation was analyzed by Heinz et al. (2004) using an individual-based simulation model. Heinz et al. found that the resulting arrival probability a_{ij} can be approximated by the following relation:

$$a_{ij} = \frac{R(d_{ij})^{N-1}}{\sum_{k(\neq i)} R(d_{ik})^{N-1}} \cdot R(d_{ij}) \qquad \text{with} \qquad R(d) = 1 - e^{-a \cdot e^{-b \cdot d}}. \tag{2.16}$$

This relation indicates that a_{ij} is proportional to $R(d_{ij})$ being a sigmoidal function of the distance d_{ij}. It describes the dispersers' potential ability to reach patches in distance d_{ij}. This term is an equivalent to the exponential terms in the preceding submodels. A sigmoidal function was found to be more appropriate to describe the effect of the variety of movement behaviors considered than a simple exponential function. The factor of proportionality in submodel (2.16), $\frac{R(d_{ij})^{N-1}}{\sum_{k(\neq i)} R(d_{ik})^{N-1}}$, is a special weight of the potential arrival probability $R(d_{ij})^{N-1}$ of patch j over the potential arrival probabilities $R(d_{ik})^{N-1}$ of all patches k. This weight reflects the rule that the dispersers stay at the first patch they reach (attraction by the patches). It is an equivalent to the pre-factors $\frac{1}{n_i}$ and $\frac{1}{N-1}$ in submodels (2.14) and (2.15), respectively. In the present case, the arrival probability a_{ij} depends on the distance d_{ij} between patch i and patch j but on the distances d_{ik} between patch i and all other patches k as well. The two function parameters a and b summarize the effect of the dispersers' species-specific movement behavior. Heinz et al. showed that submodel (2.16) is appropriate for a wide range of active movement behaviors.

In the case of larger numbers of patches N, submodel (2.16) further simplifies. If $R_{max} = \max(R(d_{ik}) : i, k)$ denotes the maximum potential arrival probability then we get

$$a_{ij} = \begin{cases} \frac{1}{\tilde{n}_i} \cdot R(d_{ij}) & \text{if } R(d_{ij}) \approx R_{max} \\ 0 & \text{else} \end{cases}. \tag{2.17}$$

where $\tilde{n}_i$ denotes the number of patches k for which $R(d_{ik}) \approx R_{max}$, i.e. which belong to the "nearest neighbors" of patch i. To understand this statement, note that $(\frac{R(d_{ik})}{R_{max}})^{N-1} \approx 1$ if $R(d_{ik}) \approx R_{max}$ and $(\frac{R(d_{ik})}{R_{max}})^{N-1} \approx 0$ if $R(d_{ik}) < R_{max}$ for larger values of N. Consequently, $\frac{R(d_{ij})^{N-1}}{\sum_{k(\neq i)} R(d_{ik})^{N-1}} = \frac{(R(d_{ij})/R_{max})^{N-1}}{\sum_{k(\neq i)} (R(d_{ik})/R_{max})^{N-1}} \approx \frac{1}{\tilde{n}_i}$ or 0. In this case, only the nearest neighbors of the individual patches i are relevant for the arrival probabilities a_{ij}.

2.4.4 Some remarks on the submodels

A comparison between the "passive" and the "active" dispersal models presented (2.12 to 2.17) reveals an important effect. In the two "passive" submodels (2.12; 2.13), the arrival probability a_{ij} exclusively depends on attributes of the two patches i and j. In the two "active" submodels (2.14; 2.16), however, a_{ij} is influenced by additional patches: in the corridor-attraction case, by all those patches k which are connected with patch i by a corridor, and in the patch-attraction case, by all other patches k or at least the nearest neighbors of patch i. This reflects a certain "competition between the patches for dispersers" caused by the fact that the actively moving dispersers are guided to or attracted by certain patches and, in this way, prevented from moving to other patches.

All the submodels presented allow an analysis of the relationship between landscape structure and metapopulation persistence through the eyes of the species' ecological profile (species-ecological attributes such as x, δ, ϵ, d_a, or d_ρ, or the dispersal type). By comparing these submodels, the robustness of certain metapopulation effects against a change in the species' ecological profile can be tested. This especially gives some idea about what metapopulation effects are generally valid and what are dependent on the species' ecology.

2.5 General remarks on the modeling framework

2.5.1 A special case: spatial homogeneity

In the following, an important special case of the patch-specific Markov chain model presented in Section 2.1 is discussed. If we assume spatial homogeneity, i.e. all the model parameters $\nu_i = \nu$, $c_{ij} = c$, $\rho_{ij} = \rho$ are independent of the patch numbers i, then the original model is equivalent to a special generalized birth and death process. Here, the number n of occupied patches is taken as state of the metapopulation, and the dynamics of the metapopulation is described by the following system of linear differential equations:

$$\frac{dP_{n,k}}{dt} = b_{n-1} \cdot P_{n-1,k} - (b_n + d_n + s_n) \cdot P_{n,k} + d_{n+1} \cdot P_{n+1,k} + s_{n+2} \cdot P_{n+2,k} \tag{2.18}$$

The corresponding "birth" rate b_n is given by the probability per time that n occupied patches colonize any empty patch. Since $c_{tot} = c \cdot (N-1)$ gives the probability that a single occupied patch colonizes any of the other $(N-1)$ patches and $(1-\frac{n-1}{N-1})$ the probability that this patch was empty, we obtain

$$b_n = c_{tot} \cdot n \cdot \left(1 - \frac{n-1}{N-1}\right). \tag{2.19}$$

The term c_{tot} is referred as total colonization rate. Since $\nu \cdot n$ gives the probability per time that one of the n occupied patches goes extinct, the "death" rate d_n results from

$$d_n = \nu \cdot n. \tag{2.20}$$

Finally, the "simultaneous death" rate s_n is given by is given by

$$s_n = \rho \cdot \nu \cdot \frac{n \cdot (n-1)}{2}. \tag{2.21}$$

This can be seen by taking into consideration that there are $\binom{n}{2} = \frac{n \cdot (n-1)}{2}$ pairs of occupied patches which simultaneously go extinct with probability per time $\rho \cdot \nu$.

In contrast to the original model, the state space is much smaller now ($N+1$ instead of 2^N states). Moreover, if the degree of correlation $\rho = 0$ (uncorrelated case), then the model completely coincides with a usual birth and death process. This model was extensively analyzed by Wissel and Stöcker (1991) and Drechsler and Wissel (1997).

The spatially homogeneous version of the original, patch-specific Markov model is rather conceptual. Because of its simplicity (only four parameters: N, ν, c, ρ), however, it allows important effects on stochastic metapopulation persistence to be derived. It is used as a reference for the analysis of the effects of spatial heterogeneity (Chapters 3 and 4).

2.5.2 On the implementation of the spatial correlation

One important "special feature" of the presented modeling framework is the incorporation of patch-specific degrees of correlation ρ_{ij} of the extinction events in the individual local populations. In this way, simultaneous extinction of several local populations can be simulated that is a first step towards modeling the effect of regional stochasticity. Note that there is no standard method of incorporating spatial correlation and regional stochasticity in metapopulation models. Therefore, it is useful to discuss some aspects of the implementation of the correlation presented in this thesis in more detail.

At a first glance, it may be surprising that the main model merely takes the pairwise correlations ρ_{ij} but not the correlations of higher order into account. But note that this is consistent with the theory of continuous time Markov processes (e.g., Feller 1970; Karlin and Taylor 1981). To consider *merely pairwise correlations is sufficient* in this case, as the following argumentation demonstrates. As is well-known, there are two equivalent ways of modeling N-dimensional, continuous time Markov processes $\mathbf{x}(t) = (x_1(t), .., x_N(t))$. The first way is using a stochastic differential equation

$$\frac{d\mathbf{x}(t)}{dt} = \mathbf{f}(\mathbf{x}(t)) + \xi(t), \tag{2.22}$$

where the stochastic part $\xi(t)$ of this so-called Langevin equation is given by a special N-dimensional Normal (Gaussian) distribution. As is known, such a distribution is completely determined by the means μ_i (here $=0$), variances σ_i^2, and pairwise correlations ρ_{ij}. All the correlations $\rho_{klm...}$ between more than two components are either zero or completely expressed in terms of all the variances σ_i^2 and pairwise correlations ρ_{ij}. The picture becomes even more clear if we shift the focus of observation from the Langevin equation to the equivalent Fokker-Planck equation given by the following partial differential equation

$$\frac{\partial P(\mathbf{x},t)}{\partial t} = -\sum_{i=1}^{N} \frac{\partial}{\partial x_i}[A_i(\mathbf{x},t)\cdot P(\mathbf{x},t)] + \frac{1}{2}\cdot\sum_{i,j=1}^{N} \frac{\partial^2}{\partial x_i \partial x_j}[B_{ij}(\mathbf{x},t)\cdot P(\mathbf{x},t)]. \tag{2.23}$$

Here, the dynamics of the resulting probability density function $P(\mathbf{x},t)$ is modelled instead of the stochastic process $\mathbf{x}(t)$ itself. The so-called "shift-functions" $A_i(\mathbf{x},t)$ and "diffusion-functions" $B_{ij}(\mathbf{x},t)$ are completely determined by the deterministic part $(\mathbf{f}(\mathbf{x}(t))$ and the variances and covariances (pairwise correlations) of the stochastic part $(\xi(t))$ of the underlying stochastic process. This shows that all the correlations between more than two components are simply not relevant for the dynamics of $P(\mathbf{x},t)$. This confirms again that considering the pairwise correlations is sufficient. But note that all these results are strongly dependent on the *assumption* that a *continuous time* Markov process is considered. The chance of incorporating all important effects of a N-dimensional stochastic process in a simple way (without having to consider any correlation between more than two components) was the reason for developing a continuous time Markov chain model.

There is another important aspect related to the issue of correlation that should be noted. An increase in a certain degree of correlation ρ_{ij} leads to an increase in the so-called *total* local extinction rate ν_i^{tot} of a currently patch i. This quantity is defined to be the sum of the local extinction rate ν_i and all the correlated extinction rates $\rho_{ij}\sqrt{\nu_i}\sqrt{\nu_j}$ taken over all the other patches j which are currently occupied, i.e.

$$\nu_i^{tot} = \nu_i + \sum_{j(\neq i; x_j=1)} \rho_{ij}\sqrt{\nu_i}\sqrt{\nu_j}. \tag{2.24}$$

This results from our assumption that a local population can go extinct for two reasons: local (within-patch dynamic) effects or regional (correlation-induced) effects. The subdivision into local and correlated extinction has the advantage that within-patch and regional drivers of local extinction can be separately analyzed in terms of their effect on the entire metapopulation dynamics. This is to the benefit of a better understanding. Moreover, all the standard submodels for single population dynamics (e.g. Goel and Richter-Dyn 1974; Leigh 1981; Nisbet and Gurney 1984; Goodman 1987; Lande 1993; Foley 1994; Wissel and Zaschke 1994; Wissel *et al.* 1994) can be used for parameterizing ν_i (note that these models exclusively address local factors of extinction). But there is also a clear disadvantage of the approach: in the field, only the total local extinction rate ν_i^{tot} can be observed and measured, but never the model parameter "local extinction rate" ν_i. But this is as usual: every approach has methodological pros and cons.

Equation (2.24) for the total local extinction rate ν_i^{tot} also brings another effect to light. Evidently, ν_i^{tot} depends on the number of occupied patches (note that the sum is taken over all patches j ($\neq i$) which are currently occupied). This is strongly consistent with a standard way of modeling environmental stochasticity on the level of local dynamics. In order to see this, we assume that the (deterministic) dynamics of the local population under consideration are characterized by linear growth with a population growth rate $(\lambda - \mu) \cdot n$ and ceiling at the carrying capacity K, where λ and μ are per capita birth and death rates. If environmental stochasticity of strength σ^2 is added and the resulting (stochastic) population dynamics are modelled as a birth and death process then the probability per time d_n that one of n individuals dies is usually modelled as $d_n = \mu \cdot n + \frac{\sigma^2}{2} \cdot n^2$ (e.g. Goodman 1987; Wissel *et al.* 1994). The quadratic term $\frac{\sigma^2}{2} \cdot n^2$ indicates that all the n individuals of the population percept the environmental fluctuations in the same way. This is the typical characteristic of environmental stochasticity. If we determine the resulting total per capita death rate μ^{tot} by calculating d_n/n, we obtain

$$\mu^{tot} = d_n/n = \mu + \tfrac{\sigma^2}{2} \cdot n. \tag{2.25}$$

This shows that μ^{tot} linearly depends on the current number of individuals n in the population, where the factor of proportionality is given by the strength of the environmental stochasticity σ^2. This indicates that there is a certain structural similarity between equation $\mu^{tot} = \mu + \frac{\sigma^2}{2} \cdot n$ and equation $\nu^{tot} = \nu + \rho\,\nu \cdot n$ in the case that n occupied patches and patch-independent parameters ($\nu_i = \nu; \rho_{ij} = \rho$) are assumed. In this sense, the implementation of the correlation of local extinction on the level of the metapopulation dynamics is consistent with the implementation of environmental stochasticity on the level of the local populations dynamics. But note that we only took correlation in the context of the extinction events into account. Additional correlation in the colonization events was ignored because a certain degree of correlation is already implicitly given. To see this, note that patches in the close neighborhood of an occupied patch have a higher chance of recolonization than more distant patches - just because of a higher dispersal success.

To summarize, all these arguments indicate that the implementation of the spatial correlation of the extinction processes is in accordance with the theory of stochastic processes and shows similarities to the implementation of the effect of environmental stochasticity and its effect on the per capita death rates on the level of the local populations.

2.5.3 Relation to other stochastic, spatially realistic, Levins-type metapopulation models

There is a huge variety of metapopulation models addressing infinite/finite numbers of patches, with/without spatial heterogeneity, with/without stochasticity, with/without spatial correlation, with/without explicit local dynamics, with/without Allee or rescue effect. There are three approaches to model stochastic metapopulation dynamics: stochastic differential equations, Monte Carlo simulations, and (continuous or discrete time) Markov chain models. The present modeling framework can be characterized as follows: stochastic, finite, spatially realistic, Levins-type, continuous time Markov chain. It has certain similarities to other stochastic, spatially realistic Levins type metapopulation models:

The modeling framework is similar to the Incidence Function Model (IFM) by Hanski (1994) widely discussed in the metapopulation literature. This model is discrete time. Although the original IFM is Levins type, it allows Allee and rescue effects to be included. The model does not take spatial correlation in the extinction processes into account.

The presented main model has similarities to the model by Akçakaya and Ginzburg (1991), a discrete time, finite Markov chain model. The model separates two phases - an extinction phase and a recolonization phase - and takes the correlation in the extinction processes into account. It has merely been applied to systems with 2 and 3 patches.

Day and Possingham (1995) adopted the idea of separating extinction and recolonization phase and developed a general, discrete time Markov chain model that is applicable to systems with arbitrary (but not too large) numbers of patches. Their model, however, ignores the spatial correlation. Day and Possingham analyzed the behavior of quasi-stationary metapopulations. They used the mean degree of patch occupancy and the survival chance $S^*(t)$ of the metapopulation as measure for metapopulation persistence.

Ovaskainen (2002) made another interesting step. He took the continuous time Markov chain model presented in this Chapter as a basis and calculated a certain weighted average $p_w(t) = \sum_i w_i \cdot x_i(t)$ over the patch occupancy states $x_i(t)$. He showed that the resulting stochastic dynamics in $p_w(t)$ can be approximated by a diffusion process, i.e. can be interpreted as a solution of a certain stochastic differential equation. In this sense, $p_w(t)$

bridges between the two different approaches of stochastic metapopulation modeling. But note that the diffusion approximation only works in case of large numbers of patches N.

2.6 References

Adler, F. R., and B. Nuernberger. 1994. Persistence in patchy irregular landscapes. *Theoretical Population Biology* 45: 41–75

Akçakaya, H.R., and Ginzburg, L.R. 1991. Ecological risk analysis for single and multiple populations. In: Seitz, A. and Loeschcke, V. (eds.) Species Conservation: A Population-Biological Approach. Birkhäuser Verlag, Basel, pp. 78–87

Akçakaya, H. R., and J. L. Atwood. 1997. A habitat-based metapopulation model of the California Gnatcatcher. *Conservation Biology* 11: 422–434

Baars, M. A., and T. H. van Dijk. 1984. Population dynamics of carabid beetles at a Dutch heathland. I. Subpopulation fluctuations in relation to weather and dispersal. *Journal of Animal Ecology* 53: 375–388

Bascompte, J., and Solé, R. V. (eds.) 1998. Modeling Spatiotemporal Dynamics in Ecology. Springer-Verlag, Berlin

Bjørnstad, O.N., Stenseth, N.C., and Saitoh, T. 1999. Synchrony and Scaling in dynamics of voles and mice in northern Japan. *Ecology* 80: 622–637

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58: 445–449

Burgman, M.A., Ferson, S., and Akçakaya, H.R. 1993. Risk assessment in conservation biology. Chapman and Hall, London

Conradt L., Bodsworth E.J., Roper T.J. and Thomas C.D. 2000. Non-random dispersal in the butterfly Maniola jurtina: implications for metapopulation models. *Proceedings of the Royal Society of London B* 267: 1505-1510.

Darroch, J.N., and Senata, E. 1965. On quasi-stationary distributions of absorbing discrete-time finite Markov chains. *Journal of Applied Probability* 2: 88-100

Day, J. R., and H. P. Possingham. 1995. A stochastic metapopulation model with variability in patch size and position. *Theoretical Population Biology* 48: 333-360 den Boer, P.J. 1981. On the survival of populations in a heterogeneous and variable environment. *Oecologia* (Berlin) 50: 39–53

Drechsler, M., and C. Wissel. 1997. Separability of local and regional dynamics in metapopulations. *Theoretical Population Biology* 51: 9–21

Etienne, R.S., and Heesterbeek, J.A.P. 2000. On optimal size and number of reserves for metapopulation persistence. *Journal of Theoretical Biology* 203: 33-50

Fahrig, L. 1992. Relative importance of spatial and temporal scales in a patchy environment. *Theoretical Population Biology* 41: 300–314

Feller, W. 1970. An Introduction to Probability Theory and its Applications. John Wiley & Sons, New York

Foley, P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. *Conservation Biology* 8: 124-137

Frank, K., and C. Wissel. 1998. Spatial aspects of metapopulation survival: from model results to rules of thumb for landscape management. *Landscape Ecology* 13: 363-379

Frank, K., Lorek, H., Kster, F., Sonnenschein, M., Wissel, C. und Grimm, V. 2003. META-X: Software for Metapopulation Viability Analysis. Springer-Verlag, Heidelberg

Gilpin, M. 1990. Extinction of finite metapopulations in correlated environments. *In* Shorocks, B. (ed.) Living in a Patchy Environment. Oxford University Press, Oxford, pp. 177–186

Goel, N. S., and N. Richter-Dyn. 1974. Stochastic Models in Biology. Academic Press, New York

Goodman, D. 1987. The demography of chance extinction. *In* Soulè, M.E. (ed.) Viable Populations for Conservation. Cambridge University Press, Cambridge, pp. 11–34

Grimm, V., and Wissel, C. 2004. The intrinsic mean time to extinction: a unifying approach to analyzing persistence and viability of populations. *Oikos* 105: 501-511

Grimm, V., N. Dorndorf, F. Frey-Roos, C. Wissel, T. Wyszomirski, and W. Arnold. 2003. Modelling the role of social behavior in the persistence of the Alpine marmot *Marmota marmota*. *Oikos* (in press)

Hanski, I. 1989. Metapopulation dynamics: Does it help to have more of the same? *Trends in Evolution and Ecology* 4: 113–114

Hanski, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* 63: 151–163

Hanski, I., and Gilpin, M. E. 1997. Metapopulation Biology: Ecology, Genetics, and Evolution, Academic Press, San Diego

Hanski, I., and Woiwod, I. P. 1993. Spatial synchrony in the dynamics of moth and aphid populations. *Journal of Animal Ecology* 62: 656–504

Hanski, I., Alho, J., and Moilanen, A. 2000. Estimating the paramters of survival and migration of individuals in metapopulations. *Ecology* 81: 239–251

Harrison, S., and Quinn, J.F. 1989. Correlated environments and the persistence of metapopulations. *Oikos* 56: 1–6

Harrison, S., Murphy, D.D. and Ehrlich, P.R. 1988. Distribution of the Bay checkerspot butterfly, *Euphydryas editha bayensis*. Evidence for a metapopulation model. *The American Naturalist* 132: 360–382

Haydon, D., and Steen, H. 1997. The effect of large- and small-scale random events on the synchrony of metapopulation dynamics: a theoretical analysis. *Proceedings of the Royal Society of London B, Biological Sciences* 264: 1375–1381

Heinz, S.K., Conradt, L., Wissel, C., and Frank, K. 2004. Dispersal behaviour in fragmented landscapes: deriving a practical formula for patch accessibility. *Landscape Ecology* (in press)

Henein, K., and Merriam, G. 1990. The elements of connectivity where corridor quality is variable. *Landscape Ecology* 4: 157–170

Holmes, E.E., Lewis, M.A., Banks, J.E., and Viet, R.R. 1994. Partial differential equations in ecology: spatial interactions and population dynamics. *Ecology* 75: 17–29

Kendall, B.E., Bjørnstad, O.N., Bascompte, J., Keitt, T.H., and Fagan, W.F. 2000. Dispersal, environmental correlation, and spatial synchrony in population dynamics. *The American Naturalist* 155: 628–636

Karlin, S., and Taylor, H. 1981. A second course in stochastic processes. Academic Press, New York

Keilson, J. 1979. Markov Chain Models - Rarity and Exponentiality (Applied Mathematical Sciences 28). Springer Verlag, New York

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist* 142: 911-927

Leigh, E. G. 1981. The average lifetime of a population in a varying environment. *Journal of Theoretical Biology* 90: 213–239

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15: 237–240

McArthur, R.H., and Wilson, E.O. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton

Mangel, M., and C. Tier. 1993. Dynamics of metapopulations with demographic stochasticity and environmental catastrophes. *Theoretical Population Biology* 44: 1–31

Moloney, K. A. 1993. Determining process through pattern: reality or fantasy. Pages 61–69 in: S. A. Levin, T. M. Powell, and J. H. Steele, eds. Patch-Dynamics (Lecture Notes in Biomathematics 96), Springer-Verlag, Berlin

Myers, J.H. and Rothman, L.D. 1995. Field experiments to study regulation of fluctuating populations. In: Cappuccino, N. and Price, P. (eds.) Population dynamics: new approaches and synthesis. Academic Press, New York, 229-251

Moilanen, A., A. T. Smith, and I. Hanski. 1998. Long-term dynamics in a metapopulation of American pika. *The American Naturalist* 152: 530–542

Moran, P.A.P. 1953. The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. *Australian Journal of Zoology* 1: 291–298

Nisbet, R. M., and Gurney, W. S. C. 1982. Modelling fluctuating populations. John Wiley & Sons, New York

Ovaskainen, 0. 2002. The effective size of a metapopulation living in a heterogeneous patch network. *The American Naturalist* 160: 612–628

Pollett, P.K. 1997. Limiting conditional distributions for metapopulation models. in A.D. McDonald, and L. McAleer (eds.) Proc. Int. Congr. on Modeling and Simulation, Vol. 2, Modeling and Simulation Society of Australia, Hobart, Australia, 807–812

Quinn, J.F. and Hastings, A. 1987. Extinction in subdivided habitats. *Conservation Biology* 1: 198–208

Ranta, E., Kaitala, V., Lindström, J., and Linden, H. 1995. Synchrony in population dynamics. *Proceedings of the Royal Society of London B, Biological Sciences* 262: 113–118

Ranta, E., Kaitala, V., and Lundberg, P. 1997. The spatial dimension in population fluctuations. *Science* 278: 1621–1623

Steen, H., Ims, R.A., and Sonerud, G.A. 1996. Spatial and temporal patterns of small-rodent population dynamics at a regional scale. *Ecology* 77: 2365–2372

Sutcliffe, O.L., Thomas, C.D., and Moss, D. 1996. Spatial synchrony and asynchrony in butterfly population dynamics. *Journal of Animal Ecology* 65: 85–95

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland

Verboom, J., Lankester, K., and Metz, J.A.J. 1991. Linking local and regional dynamics in stochastic metapopulation models. *Biol. J. Linnean Society* 42: 39–55

Vos, C. C., J. Verboom, P. F. M. Opdam, and C. J. F. Ter Braak. 2001. Toward ecologically scaled landscape indices. *The American Naturalist* 157: 24–41

Wissel, C., and S. Stöcker. 1991. Extinction of populations by random influences. *Theoretical Population Biology* 39: 315-328

Wissel, C., and S.-H. Zaschke. 1994. Stochastic birth and death processes describing minimum viable populations. *Ecological Modelling* 75/76: 193–201

Wissel, C., Th. Stephan, and S.-H. Zaschke. 1994. Modelling extinction of small populations. In Remmert, H. (ed.) Minimum viable populations. (Ecol. Studies 106), pp. 67–103

Wolfenbarger, D. O. 1946. Dispersion of small organism. *The American Midland Naturalist* 35: 1–152

Zollner P.A., and Lima S.L. 1999. Search strategies for landscape-level interpatch movement. *Ecology* 80: 1019-1030.

Part II

Analyses of stochastic metapopulation persistence

In Part I of this thesis, we have developed an appropriate modeling framework for the analysis of stochastic metapopulation persistence. This framework follows a hierarchical approach, i.e. it consists of a generic main model and a cascade of spatial submodels. While the main model focuses on the main processes of metapopulation dynamics (extinction, colonization), the submodels allow the relevant effects of the landscape structure and the species' ecology to be integrated. Mathematically spoken, the main model is a continuous time Markov chain model. Ecologically spoken, it is of the Levins-type because it does neither take Allee not rescue effects into account and includes the effects of the local dynamics merely implicitly. By using standard results from Markov chain theory, we determined adequate measures for stochastic metapopulation persistence $(c_{\mathbf{x}_0}, T_m)$. This modeling framework provides the basis for all the analyses carried out in this thesis.

Now we pass on to the main goal of this thesis. In the following four chapters, we address *important aspects of metapopulation persistence.* Special emphasis is placed on obtaining a comprehensive mechanistic understanding of the functional relationship between metapopulation persistence, the landscape structure and the species' ecology. In Chapter 4, we determine *minimum conditions* on species and patch configuration which have to be met to allow long-term metapopulation persistence. The information is crucial for understanding the ecological requirements under which management measures such as habitat connecting can have noticeable effects on metapopulation persistence at all. In Chapter 5, we address various aspects of habitat network design. Special emphasis is placed on the determination and analysis of the *optimum patch size distribution* in habitat networks with given patch configuration. One aspect of particular interest is the functional dependence of the optimum patch size distribution on both the other spatial aspects of the network structure (e.g. patch configuration, pattern of connectedness) and the species' ecology. In Chapter 6, we *compare* the *stochastic approach* to metapopulation persistence followed in this thesis with the traditional *deterministic approach* widely used in ecological theory and conservation management. We search for common effects and principle differences in the definitions and measures of persistence used and in the (absolute and relative) results obtained with the two approaches. We reveal conditions under which the two approaches are equivalent to each other and conditions under which taking the stochastic approach is vital to avoid counter-productive conclusions. Such comparisons contribute to a unified theory of metapopulation persistence urgently needed given the diversity of models in use. In all chapters, we aim at contributing to both a further development of *metapopulation theory* and the condensation of the scientific results in *tools for decision-support* in conservational landscape management. Both aims require generalization work. This leads to an additional task to be mastered in the run-up to all the analyses mentioned. In Chapter 3, we start with the deduction of an *approximation formula* T_m^a for the mean lifetime T_m of metapopulations in heterogeneous landscapes produced by the model underlying this thesis. This formula reveals how data from species and landscape have to be combined to predict metapopulation persistence. Formulas open the possibility to analyze their functional structure and to attain insight into functional interrelations and important effects on metapopulation persistence in this way. This particularly supports the generalization work required. By using the formula T_m^a for the persistence analyses in Chapters 4 to 6, we demonstrate its potential for theory building and management support.

Chapters 3 to 6 first of all aim at *answering the ecological questions* mentioned. If necessary, however, special methods will be developed to master the challenges arising in the course of the analysis work. In all chapters, we supplement the model analyses with (a) a discussion of the implications of the model results for metapopulation theory and conservational landscape management, (b) general remarks on the methods and approaches used for the analyses (where relevant), and (c) some prospects for further research.

All the chapters in Part II widely correspond with *published papers* of the candidate. "Widely" means that the Introductions are slightly modified to the benefit of a better integration of the individual chapters in the overall thesis. Since all the model analyses are based on the same model, namely that described in Chapter 2, we modified the Methods parts of the chapters as well. Whenever possible, we refer to Chapter 2. In the chapters themselves, we give a brief overview over those modeling aspects which are relevant in the context of the chapter. The Results and Discussion parts are nearly unchanged. There is one exception. In Chapter 5, the original study (optimum patch size distribution for one particular dispersal strategy) is supplemented by the analysis of additional dispersal strategies. The comparison gives rise to insights which go beyond the original results.

Chapter 3

A formula for the mean lifetime of metapopulations in heterogeneous landscapes

This chapter is mainly based on the following publication:

Frank, K. & Wissel, C. 2002. A formula for the mean lifetime of metapopulations in heterogeneous landscapes. *The American Naturalist* 159: 530–552

As was already mentioned, Part II of this thesis first of all aims at the analysis of important aspects of metapopulation persistence (e.g. minimum conditions for long-term persistence, aspects of optimum habitat network design, comparison between deterministic and stochastic approaches to metapopulation persistence). To support theory building and conservation management is one particular objective of Part II. This, however, requires generalization work. In any case, a comprehensive mechanistic understanding of the interplay between the landscape structure and the species' ecology and its effect on metapopulation persistence is crucial. This leads to a *particular challenge* that requires our attention and has to be mastered before we can pass on to the actual analysis:

In the context of metapopulations, there are at least three sources of spatial heterogeneity with influence on the main processes (extinction, colonization): (a) the patches themselves that can differ in size, shape, or habitat quality, (b) the configuration of the patches, and (c) the pattern of connectedness (e.g. arrangement of corridors or barriers, if relevant). Hence, the effect of the landscape structure on metapopulation persistence can only be fully understood if the interplay between the different spatial characteristics of the underlying habitat networks and the species' response to them are taken into account. This requires *systematic variation* work. This, however, is impeded by the *complexity* resulting from the multitude of relevant spatial factors. In the case of stochastic metapopulation dynamics, the situation is even more complex. Stochastic, spatially realistic metapopulation models are usually based on Monte Carlo simulations (e.g. Boyce 1992; Burgman *et al.* 1993; Hanski 1994; Possingham *et al.* 1994; Stelter *et al.* 1997; Vos *et al.* 2001), stochastic differential equations (e.g. Ovaskainen 2002), or on high-dimensional Markov chains (Akçakaya and Ferson 1990; Anderson 1991; Day and Possingham 1995; Frank and Wissel 1998; Etienne and Heesterbeek 2001; Ovaskainen 2002; Ovaskainen and Hanski 2004). In all cases, the decisive persistence measures ($T_m, c_{\mathbf{x}_0}$) can only numerically be determined (by statistical methods or eigensystem analysis). This *dependence on numerical work* further limits the possibilities of systematic variations.

This drawback, however, can be partly overcome. One way is to search for *approximation formulas* for the persistence measures of interest. Surely, approximation formulas have the disadvantage that they are less precise than the numerically determined values. But they also have a clear advantage: Their functional structure provides explicit insight into the interplay between the different factors and the effect on the persistence measure studied. In the result, important effects can simply be "read off", without any numerical analyses. For the mean lifetime T_m as important persistence measure, approximation formulas mereky existed for single populations and spatially homogeneous metapopulations (e.g. Goel and Richter-Dyn 1974; Leigh 1981; Nisbet and Gurney 1982; Lande 1993; Foley 1994; Wissel and Zaschke 1994; Middleton and Nisbet 1997). For spatially heterogeneous metapopulations, however, there was a complete dearth of approximation formulas for the mean lifetime T_m. The wish to fill this gap motivated the present chapter.

In the following, we deduce an approximation formula T_m^a for the mean lifetime T_m of metapopulations in heterogeneous landscapes by taking the stochastic, spatially realistic model presented in Chapter 2 as a basis. In order to achieve this goal, we develop a special method that allows the complexity of the model to be reduced and the functional structure of T_m to be disclosed. Its main idea is to look for a spatially homogeneous metapopulation with the same mean lifetime as the heterogeneous one considered. This is the same idea as that underlying the concept of the effective population size (e.g., Wright 1938; Lande and Barrowclough 1987; Gilpin 1991), widely used in population genetics, where a non-structured population exhibiting the same loss of heterozygosity as a considered structured population is sought. The method presented is based on aggregation techniques that are common in physics, but only rarely used in ecology. The resulting approximation formula T_m^a reveals how data from species and landscape have to be combined to estimate the mean lifetime. To demonstrate the applicability of this formula to real systems, we apply it to several sub-networks of the Glanville Fritillary butterfly (*Melitaea cinxia*) system on Åland, SW Finland (Hanski *et al.* 1996). By taking formula T_m^a as a basis, we derive several landscape measures for ranking habitat networks according to their effect on metapopulation persistence, some of them providing a quite good insight into the interplay between the spatial structure of habitat networks and the species' ecology. As a conlusion, we discuss the practical value of approximation formulas and the potential of using aggregation techniques as a bridge between complex realistic and simple models. We finalize with some prospects for further research.

3.1 Methods

The aim of this study is the deduction of an approximation formula for the mean lifetime T_m of metapopulations produced by the spatially realistic metapopulation model described in Chapter 2. In order to support a better understanding of both the deduction and the implications of the formula, we give a *brief overview* over all those aspects of the model and the mean lifetime T_m which are relevant in the context of the present study.

Remember that the model follows a hierarchical approach, i.e. it consists of a main model focusing on the main processes of any metapopulation dynamics (extinction, colonization) and a set of submodels for integrating landscape structure and species' ecology.

3.1.1 The main model

The main model under consideration is a continuous time Markov chain model for finite metapopulations of N patches. The model is of the Levins-type, i.e. the patches are assumed to be "empty" ($x_i = 0$) or "occupied" ($x_i = 1$). The state of the metapopulation is given by $\mathbf{x} = (x_1, ..., x_N)$ and determined by the occupancy states x_i of the patches.

The dynamics of the metapopulation are the result of changes in the occupancy states of the patches: local extinction, correlated extinction, and recolonization. Local extinction is assumed to occur with a probability per time ν_i, correlated extinction with $\rho_{ij}\sqrt{\nu_i}\sqrt{\nu_j}$, and recolonization with $\sum_{j(x_j=1)} c_{ji}$, where the sum is taken over all patches j currently occupied. The ν_is are the local extinction rates, the ρ_{ij}s the degrees of correlation, and the c_{ij}s the colonization rates. These parameters determine the transition matrix A of the Markov model (see Chapter 2) and so the stochastic dynamics of the metapopulation.

Evidently, the model does not explicitly take the within-patch dynamics into account. Instead of, all the effects of the local details that are relevant for the dynamics of the metapopulation are implicitly included and summarized in the local extinction and the colonization rates. The model does not take Allee or rescue effects into account.

The main model is close to Hanski's Incidence Function Model (IFM; Hanski 1994). The only difference is that our model is (a) continuous time, (b) does not assume a particular submodel for the extinction and colonization rates, ν_i and c_{ij}, and (c) allows the correlation between the extinction processes ρ_{ij} to be taken into account. However, by taking our model as a basis and specifying its parameters by setting ($\nu_i = e\,A_i^{-x}$, $c_{ij} = \delta\,{A_i}^b\,e^{-d_{ij}/d_a}$, $\rho_{ij} = 0$), we obtain a time-continuous version of the IFM, provided Hanski's sigmoidal formula for the yearly colonization probability $C_i = \frac{S_i^2}{S_i^2+1}$ is replaced with an exponential formula $C_i = 1 - e^{-S_i}$, where $S_i = \sum_{x_j=1} \delta\,{A_j}^b\,e^{-d_{ji}/d_a}$.

3.1.2 The submodels to include landscape structure and species' ecology

The idea to search for an approximation formula for the mean lifetime T_m of metapopulations was largely motivated by the wish to provide a tool for assessing spatially heterogeneous habitat networks in terms of their effect on metapopulation persistence. The term "habitat network" means the ensemble of the relevant patches, that is characterized by (a) the attributes of the individual patches, and (b) their spatial configuration.

In our modeling framework, any submodels can be used which relate the main model parameters $\{\nu_i, \rho_{ij}, c_{ij}\}$ to the spatial characteristics of the habitat network and the species' response to them. In Chapter 2, a whole collection of possible submodels is presented. In the present study, we use the following submodels as an example:

$$\begin{aligned}
&\textit{Local extinction rate:} & \nu_i &= e \cdot A_i^{-x}; & (3.1)\\
&\textit{Degree of correlation:} & \rho_{ij} &= e^{-d_{ij}/d_\rho}; & (3.2)\\
&\textit{Colonization rate:} & c_{ij} &= \frac{E_i}{N-1} \cdot a_{ij} & (3.3)\\
& & & \text{with} & \\
&\textit{Number of emigrants:} & E_i &= \delta \cdot A_i^b \qquad \text{and} & (3.4)\\
&\textit{Arrival probability:} & a_{ij} &= e^{-d_{ij}/d_a}. & (3.5)
\end{aligned}$$

where e is a species-specific extinction parameter, x an inverse measure for the strength of the environmental noise in the local populations, d_ρ the correlation length, i.e. the mean distance over which the correlation of extinction acts, δ the emigration rate per unit area, b an emigration parameter, and d_a the dispersal range, i.e. the mean distance a migrant is able to cover. For details or an ecological justification of these models, see Chapter 2.

3.1.3 The mean lifetime T_m as measure of persistence

In the context of the analysis of metapopulation persistence, the survival chance $S(t)$, i.e. the probability that the metapopulation is still alive at time t, is an important quantity. In this study, we focus on *quasi-stationary* metapopulations which are characterized by typical fluctuations in the occupancy pattern and a constant rate of overall extinction. The survival chance $S(t)$ of such metapopulations has the following structure:

$$S(t) = e^{-t/T_m}, \qquad (3.6)$$

where T_m is the mean lifetime of the metapopulation. This relation indicates that all effects which are relevant for the extinction process of the metapopulation are summarized in the mean lifetime T_m. Therefore, T_m as an adequate measure for the persistence of quasi-stationary metapopulations. The value of T_m is given by the negative inverse $-1/\omega$ of the subdominant eigenvalue of the transition matrix A of the Markov model. It is determined by the main model parameters $\{\nu_i, \rho_{ij}, c_{ij}\}$ (for details, see Chapter 2).

3.2 Results

To deduce an approximation formula T_m^a for the mean lifetime T_m of (quasi-stationary) metapopulations in heterogeneous landscapes is the main goal of this study. This requires to reveal the functional relationship between T_m and the model parameters $(\nu_i, E_i, a_{ij}, \rho_{ij})$.

3.2.1 The mean lifetime in the spatially homogeneous case

For two reasons, we start our investigations with the homogeneous (non-spatial) version of our model. Firstly, this allows the problem of deducing an approximation formula for the mean lifetime T_m to be approached from the simplest side. Secondly, the corresponding results can be used as a reference for the spatially heterogeneous case considered later. A metapopulation is said to be homogeneous if the following two assumptions are fulfilled:

1. The configuration is equidistant $(d_{ij} = d)$ with the consequence that $(a_{ij} = a,\ \rho_{ij} = \rho)$.
2. All patches are identical, i.e. the attributes of the corresponding local populations coincide, i.e. $(\nu_i = \nu,\ E_i = E)$.

Thus, all the relevant parameters $(\nu_i, E_i, a_{ij}, \rho_{ij})$ are independent of the patch numbers i in the homogeneous case. Furthermore, relation (3.3) shows that $c_{ij} = c = \frac{E}{N-1} \cdot a$. Hence, all main model parameters $(\nu_i, c_{ij}, \rho_{ij})$ and so the mean lifetime T_m^h of a quasi-stationary metapopulation ("h" stands for homogeneous) only depend on $(N,\ \nu,\ c = \frac{E \cdot a}{N-1},\ \rho)$. In order to deduce an appropriate approximation formula $T_m^{h,a}$ for T_m^h, a special non-linear regression analysis of the numerically determined values of T_m^h will be performed.

3.2.1.1 Deducing a formula $T_m^{h,u,a}$ for the uncorrelated homogeneous case

To get some idea about what type of non-linear regression is most promising, we start our investigations with the special case of uncorrelated extinction processes ($\rho = 0$). Under these conditions, the homogeneous version of our metapopulation model (Chapter 2) is equivalent to the finite Markov chain version of the classical Levins model (Levins 1969). Here, the state of the metapopulation is given by the number n of occupied patches, and the dynamics of the metapopulation is described as a special birth and death process $\frac{d}{dt}P_n = b_{n-1}P_{n-1} + d_{n+1}P_{n+1} - (b_n + d_n)\,P_n$. The corresponding "birth" rate b_n results from summarizing all the colonization processes that may occur if n patches are occupied. In our case, we therefore obtain $b_n = (N-n)\cdot n \cdot c_{ij} = (N-n)\cdot n\cdot c$. When doing the same with the extinction processes, we obtain a "death" rate $d_n = n \cdot \nu_i = n \cdot \nu$ (see also the model of Wissel and Stöcker (1991); Drechsler and Wissel (1997)). In the context of birth and death processes, however, there exists an exact formula for the mean lifetime of metapopulations that are initially completely occupied (i.e. $n = N$), namely $T_m^{GoRi} = \sum_{i=1}^{N}\sum_{k=i}^{N}\frac{1}{d_k}\prod_{m=i}^{k-1}\frac{b_m}{d_m}$ (Goel and Richter-Dyn 1974). This formula can be used for drawing conclusions about the mean lifetime of quasi-stationary metapopulations.

Utilizing the Goel and Richter-Dyn formula as a starting point

It is well-known that an initially completely occupied metapopulation always and very quickly reaches quasi-stationarity. Thus, the mean lifetimes of an initially completely occupied metapopulation and a quasi-stationary metapopulation nearly coincide. By applying the Goel and Richter-Dyn formula T_m^{GoRi} to our model, we therefore obtain

$$T_m^{h,u} \approx T_m^{GoRi} = \frac{1}{\nu}\cdot\sum_{i=1}^{N}\sum_{k=i}^{N}\tfrac{1}{k}\cdot\tfrac{(N-i)!}{(N-k)!}\cdot\tfrac{1}{(N-1)^{k-i}}\cdot\left(\frac{c_{tot}}{\nu}\right)^{k-i} \tag{3.7}$$

with $c_{tot} = (N-1)\cdot c$ being the probability per time that a local population colonizes any other patch. The ratio $\frac{c_{tot}}{\nu}$ gives the total mean number of colonizations a local population induces during its lifespan $T_l = \frac{1}{\nu}$. It may be interpreted as the potential colonization ability of the local populations. In our particular case $c = \frac{E\cdot a}{N-1}$, we get $\frac{c_{tot}}{\nu} = \frac{E\cdot a}{\nu}$.

Further simplification of T_m^{GoRi} by analytical approximation

Formula (3.7) is still too complex to fully understand the functional structure of $T_m^{h,u}$. By analytically approximating T_m^{GoRi} for larger values of $\frac{c_{tot}}{\nu}$, the following much simpler approximation formula $T_m^{h,u,a}$ for the mean lifetime $T_m^{h,u}$ of an uncorrelated homogeneous metapopulation can be deduced (see the calculation and relation (3.25) in the Appendix):

$$T_m^{h,u} \approx T_m^{h,u,a} = \frac{1}{\nu} \cdot e^{\frac{N}{c_{tot}/\nu}} \cdot \frac{(N-1)!}{N \cdot (N-1)^{N-1}} \cdot \left(\frac{c_{tot}}{\nu}\right)^{N-1} \tag{3.8}$$

for $\frac{c_{tot}}{\nu} > 2.5$ and $N \geq 5$. This condition does not really restrict the applicability of approximation formula $T_m^{h,u,a}$. Below these threshold values, the mean lifetime T_m is extremely low (stochastic equivalent to the Levins condition (Levins 1969)). Therefore, formula (3.8) is able to cover the whole range of ecologically relevant parameters.

The functional structure of approximation formula $T_m^{h,u,a}$ can be characterized as follows: (a) $T_m^{h,u,a}$ is proportional to the mean lifetime $T_l = \frac{1}{\nu}$ of the local populations. (b) There is some coefficient, $e^{\frac{N}{c_{tot}/\nu}}$, that approaches 1 when $\frac{c_{tot}}{\nu}$ increases. This indicates that the metapopulation approaches some asymptotic formula $T_m^{h,u,a} = \frac{1}{\nu} \cdot \frac{(N-1)!}{N \cdot (N-1)^{N-1}} \cdot (\frac{c_{tot}}{\nu})^{N-1}$ that is characterized by some power-like relationship between $T_m^{h,u,a}$ and $\frac{c_{tot}}{\nu}$.

Because of the central importance of formula (3.8) for the further analysis, it is useful to compare it with the approximation formula T_m^{NiGu} of Nisbet and Gurney (1982) widely used in metapopulation research. This gives a better understanding about what parts of the formula $T_m^{h,u,a}$ are robust against a change in the model structure and what are the consequences of different model structures for assessing metapopulation viability.

Comparison with the Nisbet and Gurney formula

Nisbet and Gurney (1982) developed a stochastic version of the classical Levins model (Levins 1969) which is based on a stochastic differential equation. The mean lifetime T_m^{NiGu} of their model is given by

$$T_m^{NiGu} = \frac{1}{\nu} \cdot e^{\frac{N/2}{c_{tot}/\nu}} \cdot e^{-N} \cdot e^{\frac{N}{2} \cdot \frac{c_{tot}}{\nu}} \tag{3.9}$$

(see formula (6.8.10) in Nisbet and Gurney 1982). By analytically comparing the functional structures of T_m^{NiGu} (see (3.9)) and our approximation formula $T_m^{h,u,a}$ (see (3.8)), certain similarities, but also some differences can be detected. (a) T_m^{NiGu} is also proportional to the mean lifetime $T_l = \frac{1}{\nu}$ of the local populations. (b) T_m^{NiGu} also contains some coefficient, $e^{\frac{N/2}{c_{tot}/\nu}}$, that approaches 1 when $\frac{c_{tot}}{\nu}$ becomes larger and that indicates the existence of some asymptotic formula $T_m^{NiGu} = \frac{1}{\nu} \cdot e^{-N} \cdot e^{\frac{N}{2} \cdot \frac{c_{tot}}{\nu}}$. (c) The major difference between T_m^{NiGu} and $T_m^{h,u,a}$ concerns the asymptotic formulas themselves. T_m^{NiGu} exhibits an exponential dependence on $\frac{c_{tot}}{\nu}$ (see the factor $e^{\frac{N}{2} \cdot \frac{c_{tot}}{\nu}}$), instead of a power-like dependence as detected for $T_m^{h,u,a}$ (see the factor $(\frac{c_{tot}}{\nu})^{N-1}$). As a consequence, T_m^{NiGu} shows a more rapid increase with $\frac{c_{tot}}{\nu}$ and predicts higher values for the mean lifetime than $T_m^{h,u,a}$. This effect is due to the fact that Nisbet and Gurney (1982) approximate the discrete numbers of occupied patches by continuous real numbers. This difference becomes crucial when small numbers of occupied patches occur, as is the case in extinction processes. This means that Nisbet and Gurney's formula T_m^{NiGu} over-estimates the persistence of metapopulations that are vulnerable to extinction and, hence, of conservation concern.

To summarize, $T_m^{h,u,a}$ and T_m^{NiGu} show the same qualitative behavior and have both a quite simple functional structure. The advantage of $T_m^{h,u,a}$ is that it overcomes the problem of overestimating the persistence of a metapopulation because it takes the discreteness of the number of occupied patches into account. All these arguments justify to take formula (3.8) as a basis for the deduction of approximation formulas for more complex situations.

3.2.1.2 Deducing a formula $T_m^{h,a}$ for the general homogeneous case

In the following, approximation formula $T_m^{h,u,a}$ (3.8) for the uncorrelated homogeneous case is used as a basis for finding a formula for the correlated homogeneous case.

Relation (3.8) indicates a power-like relationship between $(T_m^{h,u} \cdot \nu \cdot e^{-\frac{N}{c_{tot}/\nu}})$ and $\frac{c_{tot}}{\nu}$ in the uncorrelated case. Thus, we investigate whether this type of functional dependence can also be found in the correlated case. This is done by a non-linear regression analysis of the numerically determined values of T_m^h (note that the colonization probability c can be expressed in terms of $\frac{c_{tot}}{\nu}$ because $c = \frac{c_{tot}}{N-1} = \frac{1}{N-1} \frac{c_{tot}}{\nu} \nu$). As Figures 3.1A-B show, this analysis reveals a linear relationship between $\ln(T_m^h \cdot \nu \cdot e^{-\frac{N}{c_{tot}/\nu}})$ and $\ln(\frac{c_{tot}}{\nu})$ for values of $\frac{c_{tot}}{\nu} > 2.5$, each patch number N, and each correlation degree ρ. Hence, the mean lifetime

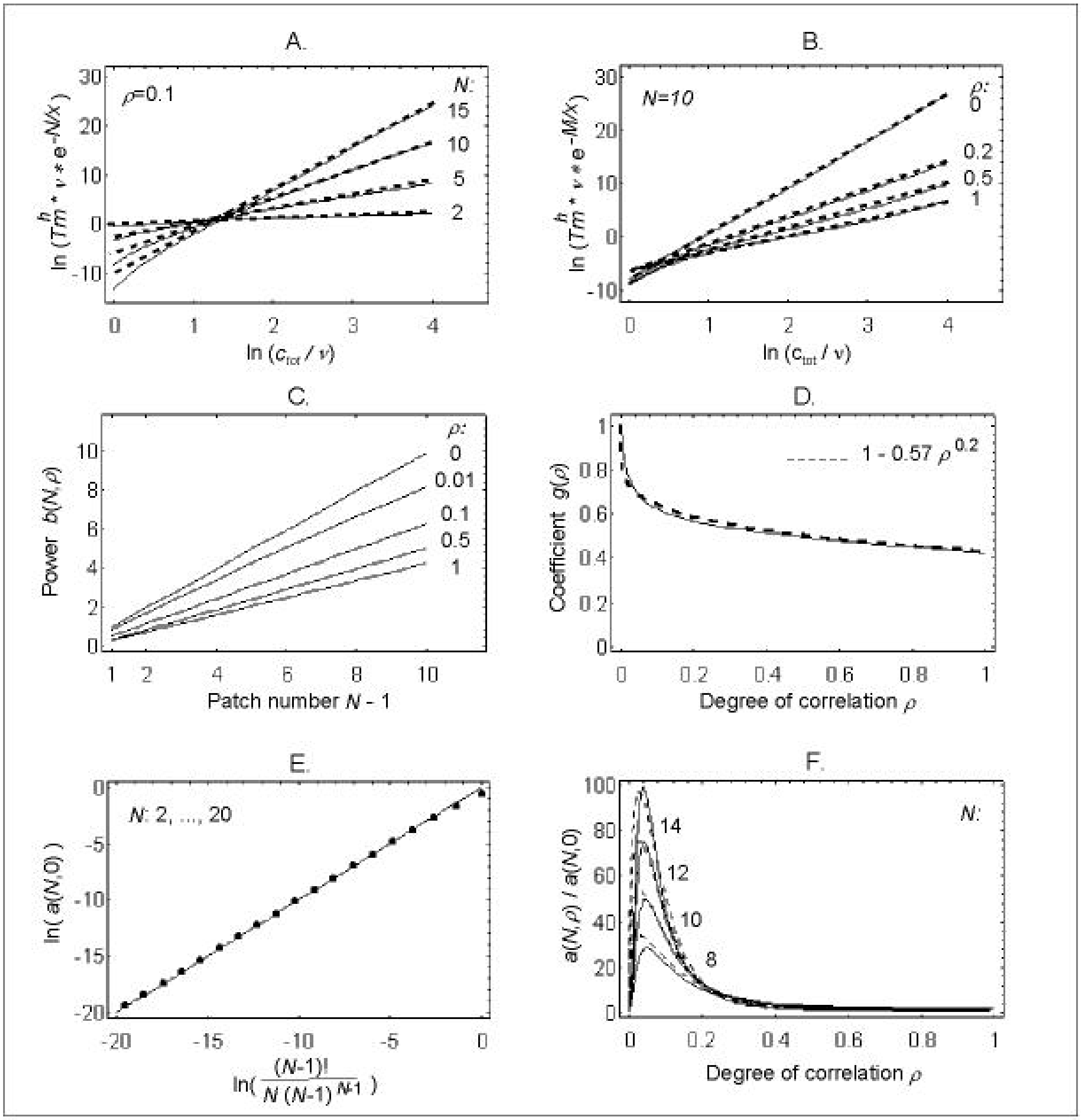

FIGURE 3.1: $\ln(T_m^h \cdot \nu \cdot e^{-\frac{N}{x}})$ with $x = \frac{c_{tot}}{\nu}$ versus $\ln(\frac{c_{tot}}{\nu})$ for the numerically determined values of the mean lifetime T_m^h of a homogeneous metapopulation with (A) $\rho = 0.1$ and different numbers of patches N and (B) $N = 10$ and different degrees of correlation ρ (full lines). In each case, a linear relationship can be detected, provided $\ln(\frac{c_{tot}}{\nu}) > 1$. This indicates that $T_m^h \cdot \nu \cdot e^{-\frac{N}{c_{tot}/\nu}} \approx a(N,\rho) \cdot (\frac{c_{tot}}{\nu})^{b(N,\rho)}$ where the power $b(N,\rho)$ is given by the slope and pre-factor $a(N,\rho) = e^{y(N,\rho)}$ by the cross-point $y(N,\rho)$ with the y-axis of the corresponding fitting line (dashed lines). (C) Power $b(N,\rho)$ versus $(N-1)$ for different values of ρ. The obvious linearity indicates that $b(N,\rho) \approx g(\rho) \cdot (N-1)$ with a coefficient $g(\rho)$ given by the slopes of the lines. (D) Coefficient $g(\rho)$ versus ρ (full line). The dashed line reveals that $g(\rho) \approx 1 - 0.57\,\rho^{0.2}$. (E) $\ln(a(N,0))$ versus $\ln(\frac{(N-1)!}{N(N-1)^{N-1}})$ indicating an identity. (F) Ratio $a(N,\rho)/a(N,0)$ versus degree of correlation ρ for different values of N. The dashed lines are given by $(1+\rho)(1 + 0.03 \cdot N^{3.6} \cdot \rho^{0.03} \cdot e^{-\rho \cdot N})$.

T_m^h of an established homogeneous metapopulation always has the following structure:

$$T_m^h \approx T_m^{h,a} = \frac{1}{\nu} \cdot e^{\frac{N}{c_{tot}/\nu}} \cdot a(N,\rho) \cdot \left(\frac{c_{tot}}{\nu}\right)^{b(N,\rho)} \qquad \text{for } \frac{c_{tot}}{\nu} > 2.5 \tag{3.10}$$

with $a(N,\rho)$ and $b(N,\rho)$ resulting from the regression analysis of the (dashed) fitting lines. Power $b(N,\rho)$ is given by the slopes of the fitting lines in Figures 3.1A-B. This quantity characteristically depends on both patch number N and correlation degree ρ. In the uncorrelated case, $b(N,0) = N-1$, as is indicated by relation (3.8). The model analysis in Figure 3.1C reveals that a linear relationship between $b(N,\rho)$ and $(N-1)$ can also be found in the correlated case. Hence, $b(N,\rho)$ can be written as $(N-1)\cdot g(\rho)$ with some coefficient $g(\rho)$ being the slope of the corresponding line. The fitting curve in Figure 3.1D indicates that $g(\rho) \approx 1 - 0.57\,\rho^{0.2}$. Thus, the functional structure of $b(N,\rho)$ is given by

$$b(N,\rho) \approx (N-1)\cdot(1-0.57\,\rho^{0.2}). \tag{3.11}$$

Pre-factor $a(N,\rho)$ in (3.10) is given by $e^{y(N,\rho)}$ with $y(N,\rho)$ being the interception point of the corresponding fitting line in Figures 3.1A-B with the y-axis. Figure 3.1E corroborates what we know from relation (3.8), namely that $a(N,0) = \frac{(N-1)!}{N\cdot(N-1)^{N-1}}$ in the uncorrelated case. In order to determine the functional structure of $a(N,\rho)$ in the correlated case, we analyze the relative ratio $a(N,\rho)/a(N,0)$ in terms of its dependence on patch number N and correlation degree ρ. Figure 3.1F reveals that there is some critical value ρ_{crit} up to which $a(N,\rho)/a(N,0)$ sharply increases with ρ. Above this value, an exponential decrease can be detected. The larger N, the stronger these effects. This qualitative description gives some idea about the structure of the underlying functional relationship. The dashed lines in Fig. 3.1F indicate that $(1+\rho)\cdot(1+0.03\cdot N^{3.6}\cdot \rho^{0.03N}\cdot e^{-\rho\cdot N})$ provides a satisfactory fit of $a(N,\rho)/a(N,0)$. Hence, the final functional structure of $a(N,\rho)$ can be described as

$$a(N,\rho) \approx \frac{(N-1)!}{N\cdot(N-1)^{N-1}}\cdot(1+\rho)\cdot(1+0.03\cdot N^{3.6}\cdot\rho^{0.03N}\cdot e^{-\rho\cdot N}) \tag{3.12}$$

To summarize, relation (3.8) together with the relations for power $b(N,\rho)$ (3.11) and pre-factor $a(N,\rho)$ (3.12) gives the desired approximation formula $T_m^{h,a}$ for the general homogeneous case. In Figs. 3.2A-B, formula $T_m^{h,a}$ (dashed lines) is compared with the numerically determined values of T_m^h (full lines). Evidently, $T_m^{h,a}$ gives a satisfactory approximation of T_m^h for various parameter values $(\frac{c_{tot}}{\nu}, N, \rho)$. This of course does not mean that $T_m^{h,a}$ is the only appropriate approximation formula. Other suitable formulas may exist.

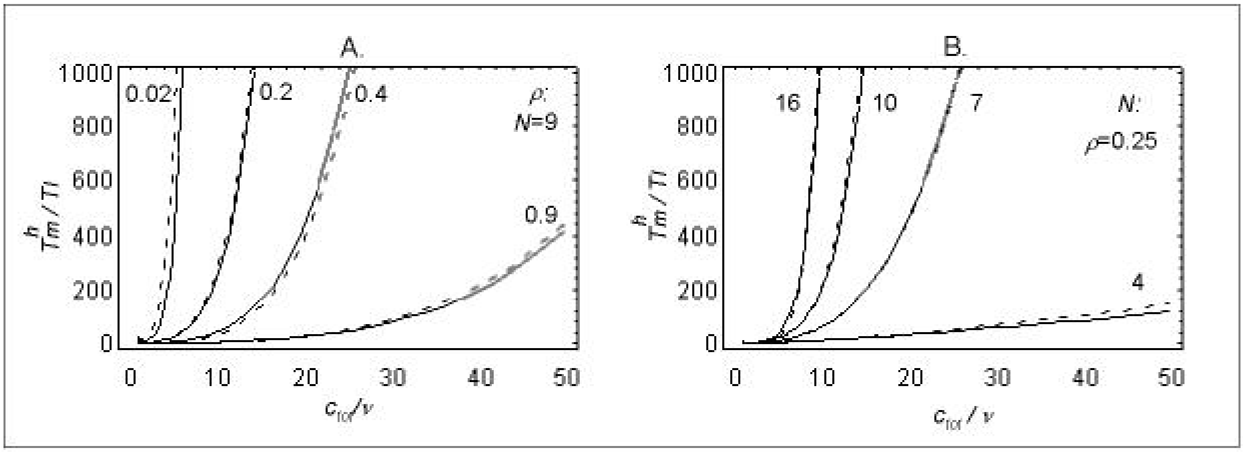

FIGURE 3.2: Ratio T_m^h/T_l versus $\frac{c_{tot}}{\nu}$ for the numerically determined values of the mean lifetime T_m^h of a homogeneous metapopulation with (A) $N = 9$ and different degrees of correlation ρ and (B) $\rho = 0.25$ and different numbers of patches N (full lines). The dashed lines give the results for the corresponding values calculated with formula $T_m^{h,a}$ in (3.10).

3.2.2 The mean lifetime in the spatially heterogeneous case

Now the basis is provided for turning to the main topic of this study: the deduction of a formula T_m^a for the mean lifetime of heterogeneous metapopulations. We present a hierarchical approach. In the first step, we show that, for every heterogeneous metapopulation, a corresponding homogeneous metapopulation of equal mean lifetime can be found. This allows us, in the second step, to extend the presented formula $T_m^{h,a}$ for the mean lifetime of homogeneous metapopulations to a formula T_m^a for the heterogeneous case.

3.2.2.1 Aggregation as a method for reducing model complexity

The main barrier to achieving the desired formula is model complexity caused by spatial heterogeneity. Hence, we have to look for a way of reducing this complexity first.

Two assumptions of spatial homogeneity (equidistant configurations; identical patches) turned the original, spatially realistic model into the much simpler non-spatial model analyzed in Section 3.2.1. Therefore, it is useful to abandon one of these assumptions after the other and to analyze in each stage how the resulting effects on the mean lifetime of a quasi-stationary metapopulation can be adequately reflected by the non-spatial model.

In the following, we focus on metapopulations with a fixed number of patches N. In this case, the non-spatial model is completely described by four parameters (ν, E, r, ρ). When abandoning the assumptions of homogeneity, i.e. turning to heterogeneous configurations or non-identical patches, an "individualization" of the parameters $(\nu_i, E_i, a_{ij}, \rho_{ij})$ occurs that now depend on the individual patch numbers i and j. These findings give rise to the following method of reducing the complex spatially realistic model to the simpler non-spatial one. The main idea underlying this method is to look for opportunities to aggregate all individual parameters p_i (p_i stands for ν_i, E_i, a_{ij} or ρ_{ij}) such that the non-spatial model together with the resulting aggregated parameter $p = p_{agg}$ produces nearly the same mean lifetime as the original spatially realistic one, i.e. $T_m^h(p_{agg}) \approx T_m(p_i)$. Several standard aggregations (e.g. taking arithmetic, geometric, harmonic or weighted means of p_i, or mixtures thereof) will be tested to reveal which is best for fitting T_m. Exactly the same idea underlies the concept of the effective population size, N_e, widely used in population genetics (Wright 1938; Lande and Barrowclough 1987; Gilpin 1991). In this case, one is interested in the population size N_e of the ideal (non-structured) population which shows the same loss of heterozygosity as a considered structured population.

Abandoning the assumption of equidistant configurations

In the following, we turn from equidistant to heterogeneous configurations and look for opportunities to aggregate the parameters affected (a_{ij}, ρ_{ij}). To cover a large range of natural configurations, extreme examples are considered: the one-dimensional "chain" (Fig. 3.3A) and the two-dimensional "array" (Fig. 3.3B). Both configurations are scaled by the distance d between the central patch and its nearest neighbors. This allows each configuration to be characterized by its scale and its relative topology. The dashed lines in Figures 3.3C-D reveal for each configuration type that a quasi-stationary metapopulation of identical patches with parameters $(\nu, E, a_{ij}, \rho_{ij})$ has nearly the same mean lifetime as a quasi-stationary homogeneous metapopulation with parameters (ν, E, a_{agg}, ρ_{agg}), where the aggregated parameters a_{agg} and ρ_{agg} for the probabilities of arrival a_{ij} and the degrees of correlation c_{ij} are given by the following characteristic means:

$$a_{agg} = \prod_{i=1}^{N} \left(\tfrac{1}{N-1} \sum_{j(\neq i)} a_{ij}\right)^{\frac{1}{N}} \quad , \quad \rho_{agg} = \tfrac{1}{N(N-1)} \sum_{i=1}^{N} \sum_{j(\neq i)} \rho_{ij}. \tag{3.13}$$

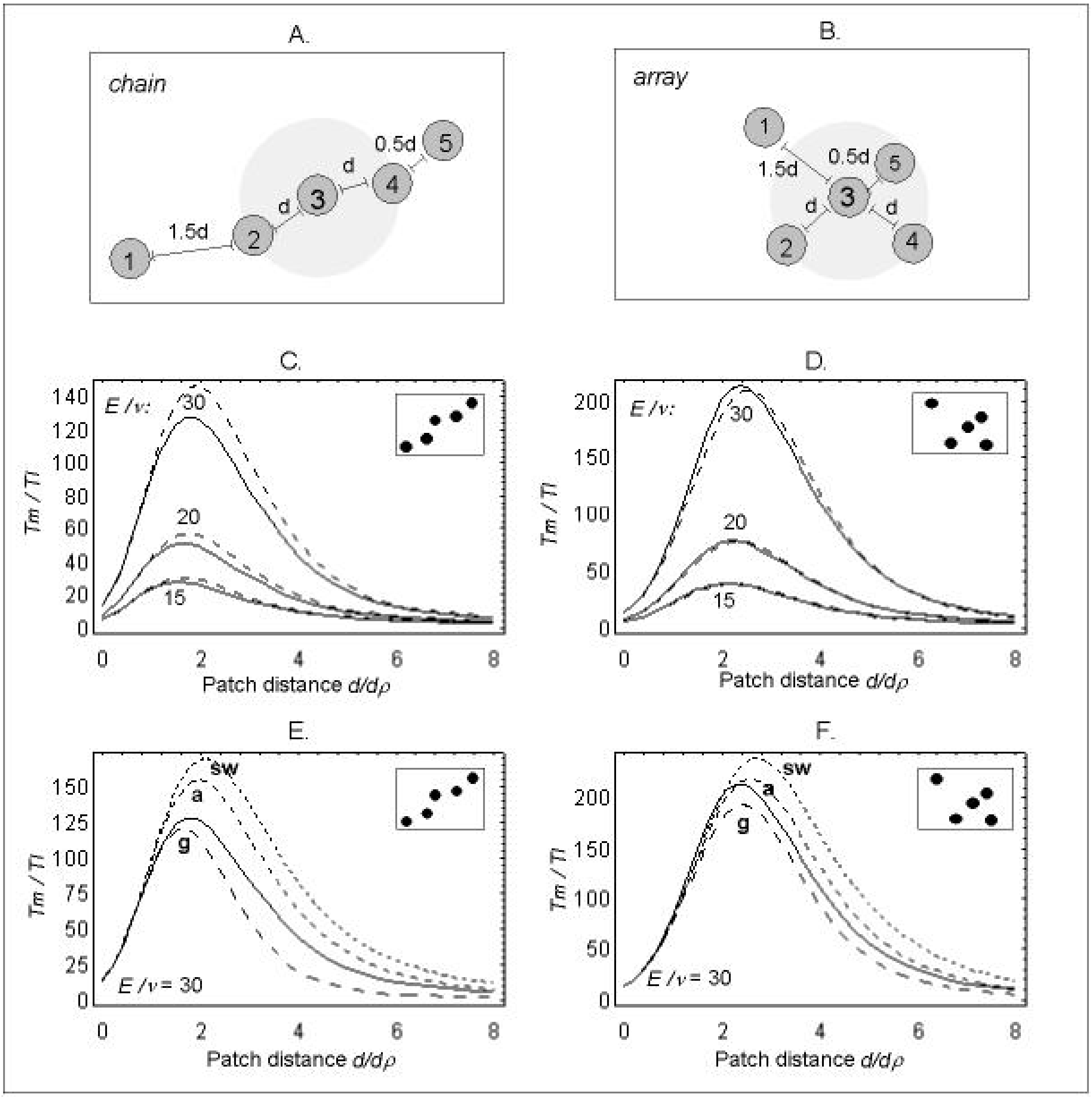

FIGURE 3.3: (A) One-dimensional "chain" and (B) two-dimensional "array". (C-F) Ratio T_m/T_l versus patch distance d/d_ρ for the numerically determined mean lifetime T_m of a metapopulation living in chain (C, E) and array (D, F) for different values of E/ν and long-distance dispersal ($d_a/d_\rho = 4$) (full lines; all distances are measured in units of the correlation length d_ρ). The dashed lines belong to a homogeneous metapopulation with parameters $(\nu, E, a_{agg}, \rho_{agg})$ where ρ_{agg} is the aggregated degree of correlation given in (3.13). The aggregated arrival probability a_{agg} used in (C, D) results from aggregation rule (3.13), while in (E, F) a geometric ("g"), an arithmetic ("a") and a self-weighted arithmetic mean ("sw") have been used for aggregation.

Other standard aggregations have also been tested. The results for aggregating the probabilities of arrival a_{ij} are displayed in Figures 3.3E-F. It can be seen that the usual geometric mean ("g"; $(\prod\prod a_{ij})^{\frac{1}{N(N-1)}}$) under-estimates the mean lifetime T_m, while both the usual arithmetic ("a", $\frac{1}{N(N-1)}\sum\sum a_{ij}$) and the self-weighted arithmetic mean ("sw", $\sum \frac{a(i)}{\sum a(k)}\, a(i)$ with $a(i) = \frac{1}{N-1}\sum_{j(\neq i)} a_{ij}$) over-estimate T_m. These effects are the stronger, the more heterogeneous the configuration is (compare chain (Fig. 3.3E) with array (Fig. 3.3F)). The result on the self-weighted mean is of particular importance because this aggregation is widely used in the theory of infectious diseases (Anderson and May 1991) and in the context of persistence of metapopulations with identical patches (Adler and Nuernberger 1994; Hanski and Ovaskainen 2000). In both fields, however, deterministic models have been taken as a basis. The over-estimation of the mean lifetime T_m documented in Figures 3.3E-F reveals that the self-weighted mean does not correctly reflect the effects of spatial configuration if stochasticity is taken into account. The aggregation rules presented here (relation (3.13)) are found to be best for fitting T_m.

Abandoning the assumption of identical patches

We turn from identical to non-identical patches and look for aggregations of the local population parameters (ν_i, E_i). A first attempt in this direction was already made in a previous study (Frank and Wissel 1998). Here, a usual geometric mean was taken to aggregate the numbers of emigrants, E_i, and the extinction rates, ν_i. It came out that the aggregation rule E_{agg} only fitted well if the variation in the numbers of emigrants E_i was not too high. Hence, a more sophisticated aggregation rule is needed to cover the range of high variation as well. We demonstrate how an appropriately modified formula can be derived by utilizing the knowledge of the qualitative behavior of the mean lifetime T_m.

In order to clarify the behavior of the mean lifetime T_m in the case of high variation in the numbers of emigrants E_i, we perform the following model experiment. We increase the value for a single patch (say E_1) while keeping the values for all other patches constant. The effect on T_m is shown in Fig. 3.4A where different sets of parameter values for the E_is as in Table 3.I are analyzed and the configuration "chain" considered before is taken as a basis. In each case, the mean lifetime T_m reaches a certain saturation value T_m^{sat} when E_1 becomes sufficiently large. This saturation behavior is a reflection of the fact that the metapopulation cannot take any additional benefit from a further enlargement of E_1. The number of emigrants E_1 is already so high that the recolonization of all other patches is safe, but only as long as patch 1 is occupied. In this situation, the mean lifetime T_m much more depends on what happens if patch 1 becomes empty than on E_1. Thus, the result in Fig. 3.4B is not surprising, indicating that the saturation value T_m^{sat} for the mean lifetime is essentially proportional to some power of $(\mathrm{IN}(1) \cdot \prod_{i(\neq 1)} E_i)$ with IN(1) being the total recolonization chance $\mathrm{IN}(1) = \sum_{j(\neq 1)} c_{j1}$ of patch 1, i.e. the sum over the colonization rates $c_{j1} = \frac{E_j}{N-1} \cdot a_{j1}$ from all other patches j. Such a saturation behavior, however, cannot on principle be reflected by a geometric mean $E_{agg} = \prod_{i=1}^{M} E_i^{\frac{1}{N}}$ over the numbers of emigrants E_i, because it shows unlimited growth with E_1.

To obtain an idea about how to modify E_{agg}, we look for standard aggregations that allow any sort of saturation to be reflected. The harmonic mean $H(x,y) = (\frac{1}{2}(\frac{1}{x} + \frac{1}{y}))^{-1} = \frac{2xy}{x+y}$ of two numbers x and y provides an aggregation of the desired type (note that $H(x,y)$ converges to $2y$ if x becomes very large). This roughly explains why it is useful to take

$$E_{agg} = \prod_{i=1}^{N} \sqrt{\left(\frac{1}{2}\left(\frac{1}{E_i^{\,2}} + \frac{1}{(\sum_{j(\neq i)} w_j^i\, E_j)^2}\right)\right)^{-1}}^{\frac{1}{N}} \tag{3.14}$$

as a candidate for aggregating the numbers of emigrants E_i. The weights w_j^i are given by

$$w_j^i = \frac{a_{ji}}{\sum_{n(\neq i)} a_{ni}}. \tag{3.15}$$

TABLE 3.I:

Different sets of numbers of emigrants E_i for the local populations 2 to 5 of the metapopulation living in the "chain" (Fig. 3.3A). These parameter sets underly the study in Figure 3.4.

	A	**B**	**C**	**D**	**E**	**F**
E_2	10	5	64	20	20	5
E_3	11	10	6	21	40	100
E_4	12	50	20	22	5	50
E_5	13	20	8	23	50	20

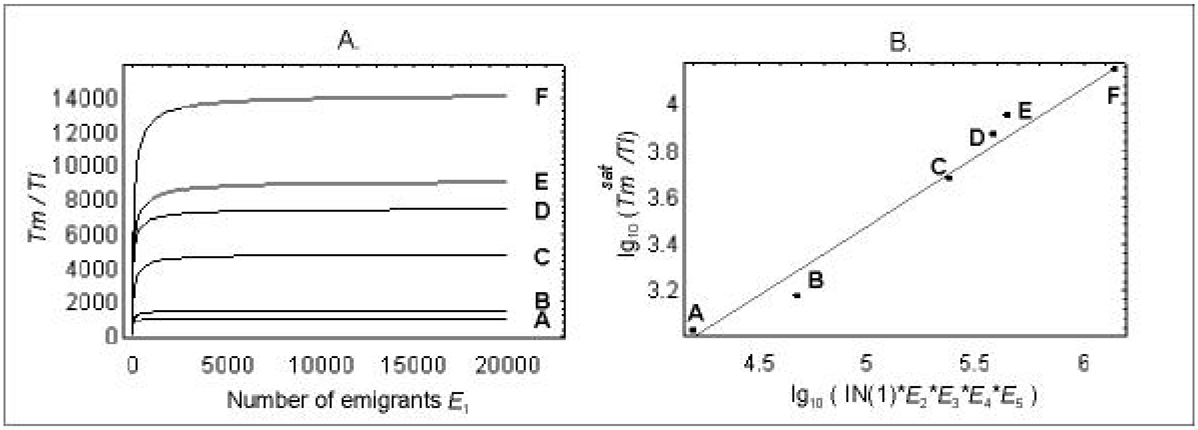

FIGURE 3.4: (A) Ratio T_m/T_l for the numerically determined mean lifetime T_m of the metapopulation versus the number of emigrants E_1 for the "chain" with $d/d_\rho = 4$, different sets of the numbers of emigrants E_i of all other patches as in Table 3.I, and a local extinction rate $\nu = 0.1$. The convergence to a saturation value T_m^{sat}/T_l is obvious. (B) $\lg_{10}(T_m^{sat}/T_l)$ versus $\lg_{10}(\mathrm{IN}(1)\, E_2\, E_3\, E_4\, E_5)$ for the parameter sets analyzed in Fig. 3.4A with IN(1) being the total recolonization chance of patch 1 given by $\mathrm{IN}(1) = \sum_{j(\neq 1)} = \frac{E_j}{N-1} \cdot a_{j1}$. The relationship between the two quantities can be characterized as nearly linear. This means that the saturation value T_m^{sat}/T_l is essentially proportional to a certain power of $(\mathrm{IN}(1)\, E_2\, E_3\, E_4\, E_5)$.

The only thing we have to do is to show that aggregation rule E_{agg} (5.3) really does provide a good qualitative and quantitative fit of the mean lifetime T_m. The calculation in the Appendix 3.5.2 reveals that E_{agg} converges to $\sqrt{2}\cdot(\frac{N-1}{\sum_{n(\neq 1)} a_{n1}})^{\frac{1}{N}} \cdot (\mathrm{IN}(1) \cdot \prod_{i(\neq 1)} E_i)^{\frac{1}{N}}$ if the value for E_1 becomes very large. When applying the mean lifetime T_m^h of the non-spatial model to the aggregated parameter E_{agg}, we see that T_m^h converges to a limit value that is proportional to $(\mathrm{IN}(1) \cdot \prod_{i(\neq 1)} E_i)^{\frac{b(N,\rho)}{N}}$ (remember the power-like dependence of $T_m^h(E_{agg})$ on E_{agg}; see (3.10)). This is exactly the effect we have seen in Figure 3.4. Hence, E_{agg} qualitatively correctly reflects the saturation behavior of the mean lifetime T_m.

Figures 3.5A-D finally reveal that the modified aggregation rule E_{agg} also provides a very good quantitative fit of the mean lifetime T_m. The dashed lines indicate for each of the considered configurations and different sets of local settings (ν_i, E_i) showing a high variation as in Table 3.II that a metapopulation with parameters $(\nu_i, E_i, a_{ij}, \rho_{ij})$ has nearly the same mean lifetime as a homogeneous metapopulation with parameters $(\nu_{agg}$, E_{agg}, a_{agg}, $\rho_{agg})$ where a_{agg}, ρ_{agg} and E_{agg} are as in relation (3.13) and (5.3), while the aggregation ν_{agg} of the extinction probabilities ν_i is given by the usual geometric mean

$$\nu_{agg} = \prod_{i=1}^{N} {\nu_i}^{\frac{1}{N}}. \tag{3.16}$$

The presented formulas (3.13; 5.3; 3.16) cover a wide range of metapopulations, including those with high variation in their characteristics $(\nu_i, E_i, a_{ij}, \rho_{ij})$.

A first conclusion

The preceding results give rise to a first conclusion that provides a better understanding of both the next steps in our study and metapopulation persistence in heterogeneous landscapes in general. As the non-spatial model indicates, there is one quantity of particular importance for metapopulation persistence, the potential colonization ability $\frac{c_{tot}}{\nu} = \frac{E \cdot a}{\nu}$ of the local populations, that summarizes all the effects of the turnover dynamics. Its spatial pendant is $(\frac{c_{tot}}{\nu})_{agg} = \frac{E_{agg} \cdot a_{agg}}{\nu_{agg}}$ that can simply be determined by the aggregation rules presented (3.13; 5.3; 3.16). The calculation in Appendix 5.3.3 shows that

$$\left(\frac{c_{tot}}{\nu}\right)_{agg} = \prod_{i=1}^{N} \sqrt{\frac{1}{\frac{1}{2} \cdot \left(\left(\frac{\mathrm{OUT}(i)}{\nu_i}\right)^{-2} + \left(\frac{\mathrm{IN}(i)}{\nu_i}\right)^{-2} \right)}}^{\,\frac{1}{N}}, \tag{3.17}$$

where the quantities $\mathrm{OUT}(i)$ and $\mathrm{IN}(i)$ in the product have the following structure:

$$\mathrm{OUT}(i) = \sum_{j(\neq i)} c_{ij} \quad \text{and} \quad \mathrm{IN}(i) = \sum_{j(\neq i)} c_{ji}, \tag{3.18}$$

TABLE 3.II

The specific local characteristics $\{(\nu_i, E_i)\}$ of the metapopulation analyzed in Figure 3.5.

G		**H**		**I**		**J**		**K**		**L**	
E_i	ν_i	E_i	ν_i	E_i	ν_i	E_i	ν_i	E_i	ν_i	E_i	ν_i
5	0.1	5	0.15	5	0.5	12	0.1	40	0.1	10	0.1
6	0.2	6	0.05	6	0.01	620	0.2	20	0.2	20	0.2
7	0.3	7	0.1	7	0.2	6	0.3	30	0.3	1000	0.3
8	0.4	8	0.08	8	0.3	20	0.4	50	0.4	5	0.4
9	0.05	9	0.2	9	0.1	8	0.05	10	0.05	100	0.05

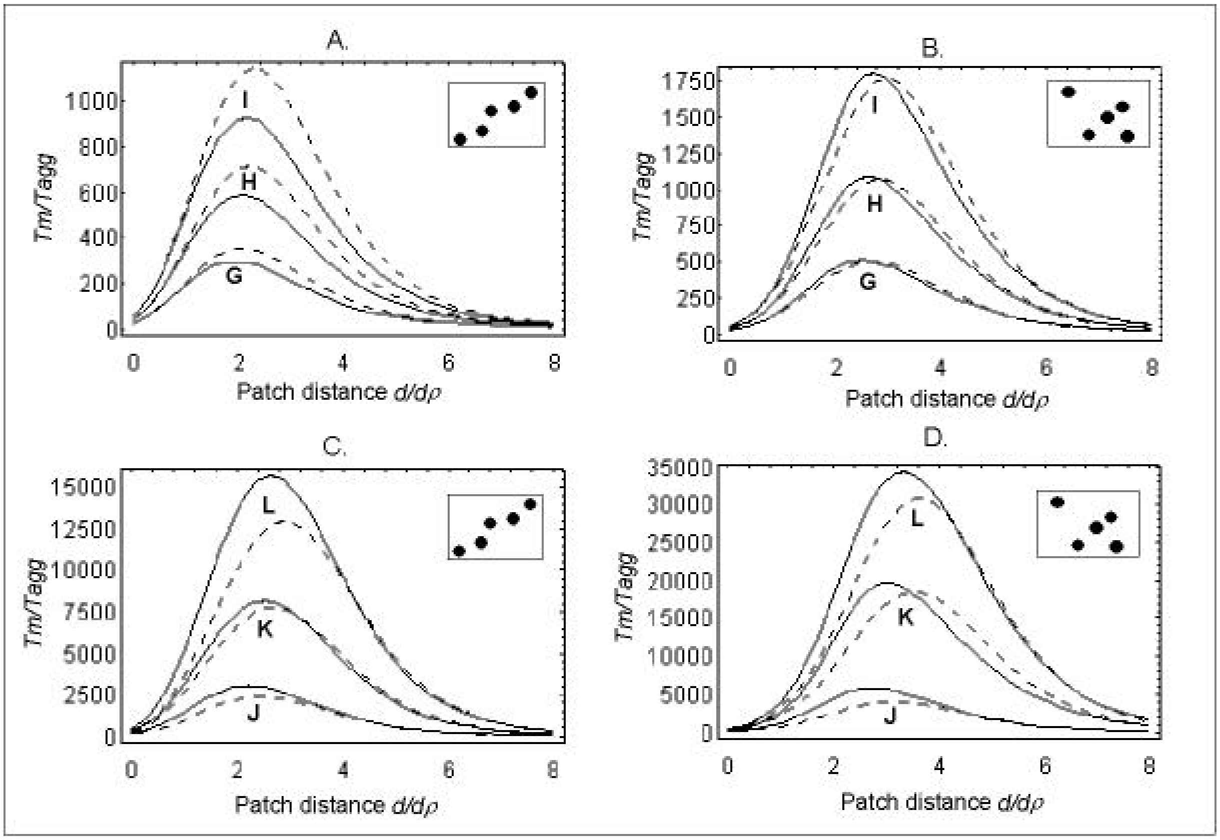

FIGURE 3.5: Ratio T_m/T_{agg} with $T_{agg} = 1/\nu_{agg}$ versus patch distance d/d_ρ for the numerically determined mean lifetime T_m of a metapopulation in chain (A, C) and array (B, D), long-distance dispersal and local settings as in Table 3.II (full lines; for the configurations see Figure 3.3). The dashed lines belong to a homogeneous metapopulation with parameters $(\nu_{agg}, E_{agg}, a_{agg}, \rho_{agg})$ resulting from the aggregation rules given in (3.13; 5.3; 3.16).

where c_{ij} are the colonization rates from the main model. This shows that, although the aggregation formulas for the components ν_{agg}, E_{agg}, and a_{agg} are sophisticated, the resulting ratio $(\frac{c_{tot}}{\nu})_{agg} = \frac{E_{agg} \cdot a_{agg}}{\nu_{agg}}$ is quite simple: a geometric mean over the harmonic means (term under the square root) of two ratios, $(\frac{\mathrm{OUT}(i)}{\nu_i})^2$ and $(\frac{\mathrm{IN}(i)}{\nu_i})^2$, that can be determined by taking sums over the rows (OUT(i)) and columns (IN(i)) of the matrix (c_{ij}) of the colonization rates and dividing them by the extinction rates ν_i.

The aggregated quantity $(\frac{c_{tot}}{\nu})_{agg}$ is very intuitive. Ratio $\frac{\mathrm{OUT}(i)}{\nu_i}$ equals the total mean number of colonizations local population i is able to induce during its lifespan $T_i = \frac{1}{\nu_i}$. It may be interpreted as its potential colonization ability. Ratio $\frac{\mathrm{IN}(i)}{\nu_i}$ may be interpreted as a measure for "being in the play" that can result from both a high chance of recolonization after an extinction (IN(i)) or a long mean lifetime ($\frac{1}{\nu_i}$). This allows us to interpret $(\frac{c_{tot}}{\nu})_{agg}$ as the effective colonization ability of the local populations. This quantity covers both aspects of the colonization process: "colonizing" and "becoming recolonized".

The ratios $\frac{\mathrm{IN}(i)}{\nu_i}$ and $\frac{\mathrm{OUT}(i)}{\nu_i}$ can also be used to formulate the limits of applicability of the aggregation rules (3.13; 5.3; 3.16; 3.17). We found in a more detailed model analysis that these rules are only valid if the harmonic mean $z_i = (\frac{1}{2}((\frac{\mathrm{OUT}(i)}{\nu_i})^{-2} + (\frac{\mathrm{IN}(i)}{\nu_i})^{-2}))^{-1/2}$ is greater or equal than $\sqrt{2}$ for every patch i. If this condition is not met by certain patches j because they are too rarely occupied ($\frac{\mathrm{IN}(j)}{\nu_j}$ is low) or too weak for colonization ($\frac{\mathrm{OUT}(j)}{\nu_j}$ is low), then aggregation rule (3.17) has to be replaced by $(\frac{c_{tot}}{\nu})_{agg} = \prod_{i=1}^{N} \max(\sqrt{2}, z_i)^{1/N}$. In this modified rule, only patches i with values $z_i \geq \sqrt{2}$ contribute to $(\frac{c_{tot}}{\nu})_{agg}$ reflecting that the metapopulation does not markedly benefit from the critical patches.

Finally, since formula (3.17) is completely formulated in the "language" of the main model parameters (ν_i, c_{ij}), it gives some idea of how to aggregate the parameters in situations which differ from the particular case ($c_{ij} = \frac{E_i}{N-1} \cdot a_{ij}$; see (3.3)) considered here.

Evidence for the ecological plausibility of the aggregation rules

Because of the central importance for further analysis of the aggregated parameters presented ($\nu_{agg}, \rho_{agg}, (\frac{c_{tot}}{\nu})_{agg}$), we look for arguments which ecologically underpin the mathematically deduced findings. (a) Most of the aggregations presented show a multiplicative structure. This multiplicativity is a reflection of the inherent feedback between the local populations (each local population influences the chance of all other local populations of being involved and contributing to metapopulation persistence). (b) The presented aggregation rules ν_{agg} and ρ_{agg} for the characteristics of extinction are independent of the parameters of colonization (c_{ij}, E_i, a_{ij}). This finding is a consequence of our assumption that rescue effects do not play a perceptible role (Chapter 2), indicating that the exchange of individuals is of no bearing as far as the extinction of local populations is concerned. (c) The plausibility of $(\frac{c_{tot}}{\nu})_{agg}$ has already been discussed. (d) Evidence for the reasonableness of the aggregations found is also provided by the fact that whole functional relationships between the mean lifetime T_m and certain model parameters are qualitatively correctly and quantitatively sufficiently reflected (e.g. the relationship between T_m

and patch distance d/d_ρ; saturation behavior of T_m when the number of emigrants E_k of a single patch k increases). This is extremely important for understanding the dynamics.

To summarize, our model results reveal that it really is possible to aggregate all relevant parameters p_i (p_i stands for $(\nu_i, E_i, a_{ij}, \rho_{ij})$) such that the non-spatial model applied to the aggregated parameters p_{agg} produces nearly the same mean lifetime as the original, spatially realistic one, i.e. $T_m^h(p_{agg}) \approx T_m(p_i)$. These aggregated parameters p_{agg} are comparable with the effective population size N_e well-known from population genetics. Compared to the quite elegant classical formulas for the effective population size (e.g. $N_e = 2\,(\frac{1}{2}(\frac{1}{N_f} + \frac{1}{N_m}))^{-1}$ with N_f and N_m being the number of females and males (Wright 1938)), the aggregation rules for the metapopulation parameters presented here (3.13; 5.3; 3.16; 3.17) are rather complex. This is due to the fact that there a different sorts of spatial factors interacting with each other and influencing all metapopulation processes.

3.2.2.2 The approximation formula T_m^a for the heterogeneous case

Now the basis is provided for addressing the deduction of an approximation formula T_m^a for the mean lifetime T_m of a quasi-stationary metapopulation. As we have seen, a quasi-stationary metapopulation with parameters $(\nu_i, E_i, a_{ij}, \rho_{ij})$ has the same survival chance as a quasi-stationary homogeneous metapopulation with parameters $(\nu_{agg}, E_{agg}, a_{agg}, \rho_{agg})$. Hence, we have an equality between the corresponding mean lifetimes T_m and T_m^h:

$$T_m\,(N,\,\nu_i,\,E_i,\,a_{ij},\,,\,\rho_{ij}) \;\approx\; T_m^h\,(N,\,\nu_{agg},\,E_{agg},\,a_{agg},\,\rho_{agg}). \qquad (3.19)$$

For the mean lifetime T_m^h of homogeneous metapopulations, however, an approximation formula $T_m^{h,a}$ already exists (see (3.10)). By applying $T_m^{h,a}$ to the aggregated parameters $(\nu_{agg}, (\frac{c_{tot}}{\nu})_{agg} = \frac{E_{agg}\cdot a_{agg}}{\nu_{agg}}, \rho_{agg})$, an approximation formula T_m^a for the mean lifetime T_m of any (homogeneous or heterogeneous) metapopulations results:

$$T_m^a \;:=\; T_m^{h,a}\left(N, \nu_{agg},\, (\tfrac{c_{tot}}{\nu})_{agg},\, \rho_{agg}\right) \quad \text{provided} \quad (\tfrac{c_{tot}}{\nu})_{agg} > 2.5\,,\; N \geq 5. \qquad (3.20)$$

For an overview over the exact functional structure of T_m^a and its "ingredients" see Table 3.III. Despite the latter conditions, formula T_m^a covers a large range of the ecologically interesting situations for the same arguments as in the non-spatial case (Sec. 3.2.1.1).

Table 3.III

Overview over the “ingredients” of the approximation formula T_m^a presented

The approximation formula T_m^a for the mean lifetime T_m of a metapopulation

$$T_m^a(N, \nu_i, c_{ij}, \rho_{ij}) \;:=\; T_m^{h,a}\,(N, \nu_{agg},\, (\tfrac{c_{tot}}{\nu})_{agg},\, \rho_{agg})$$

consisting of two major components:

the approximation formula $T_m^{h,a}$ for the homogeneous case

$$T_m^{h,a}(N, \nu,\, \tfrac{c_{tot}}{\nu},\, \rho) \;:=\; \tfrac{1}{\nu} \cdot e^{\frac{N}{c_{tot}/\nu}} \cdot a(N,\rho) \cdot \left(\tfrac{c_{tot}}{\nu}\right)^{b(N,\rho)}$$

with

$$a(N,\rho) = \tfrac{(N-1)!}{N \cdot (N-1)^{N-1}} \cdot (1+\rho) \cdot (1 + 0.03 \cdot N^{3.6} \cdot \rho^{0.03N} \cdot e^{-\rho \cdot N}),$$

$$b(N,\rho) = (N-1) \cdot (1 - 0.57\,\rho^{0.2})$$

and all the relevant aggregated parameters

$$\nu_{agg} \;=\; \prod_{i=1}^{N} {\nu_i}^{\frac{1}{N}},$$

$$\left(\frac{c_{tot}}{\nu}\right)_{agg} = \prod_{i=1}^{N} \max\left(\sqrt{2}, \sqrt{\left(\frac{1}{2}\left(\left(\frac{\sum_{j(\neq i)} c_{ij}}{\nu_i}\right)^{-2} + \left(\frac{\sum_{j(\neq i)} c_{ji}}{\nu_i}\right)^{-2}\right)\right)^{-1}}\,\right)^{\frac{1}{N}},$$

$$\rho_{agg} = \tfrac{1}{N(N-1)} \cdot \sum_{i=1}^{N} \sum_{j(\neq i)} \rho_{ij}$$

Testing the “correctness” of the deduced approximation formula T_m^a

Before we start to analyze the functional structure of formula (3.20), we check its ability to approximate the mean lifetime T_m produced by the model and to reproduce well-known qualitative effects on metapopulation persistence.

In Figures 3.6A-B, values calculated with formula (3.20) are compared to the numerically determined values for the mean lifetime T_m, where the configurations and parameter sets analyzed in Figures 3.3C-D and 3.5A-D are taken as a basis and different patch distances d/d_ρ are considered. Evidently, T_m^a provides a satisfactory quantitative fit of T_m.

In order to demonstrate that formula T_m^a also works in situations with larger numbers of patches N and more realistic configurations, we applied it to 72 sub-networks of the Glanville Fritillary (*Melitaea cinxia*) system on the Åland islands, SW Finland (Hanski *et al.* 1996). These sub-networks show a high variation in patch number (2 to 10), patch

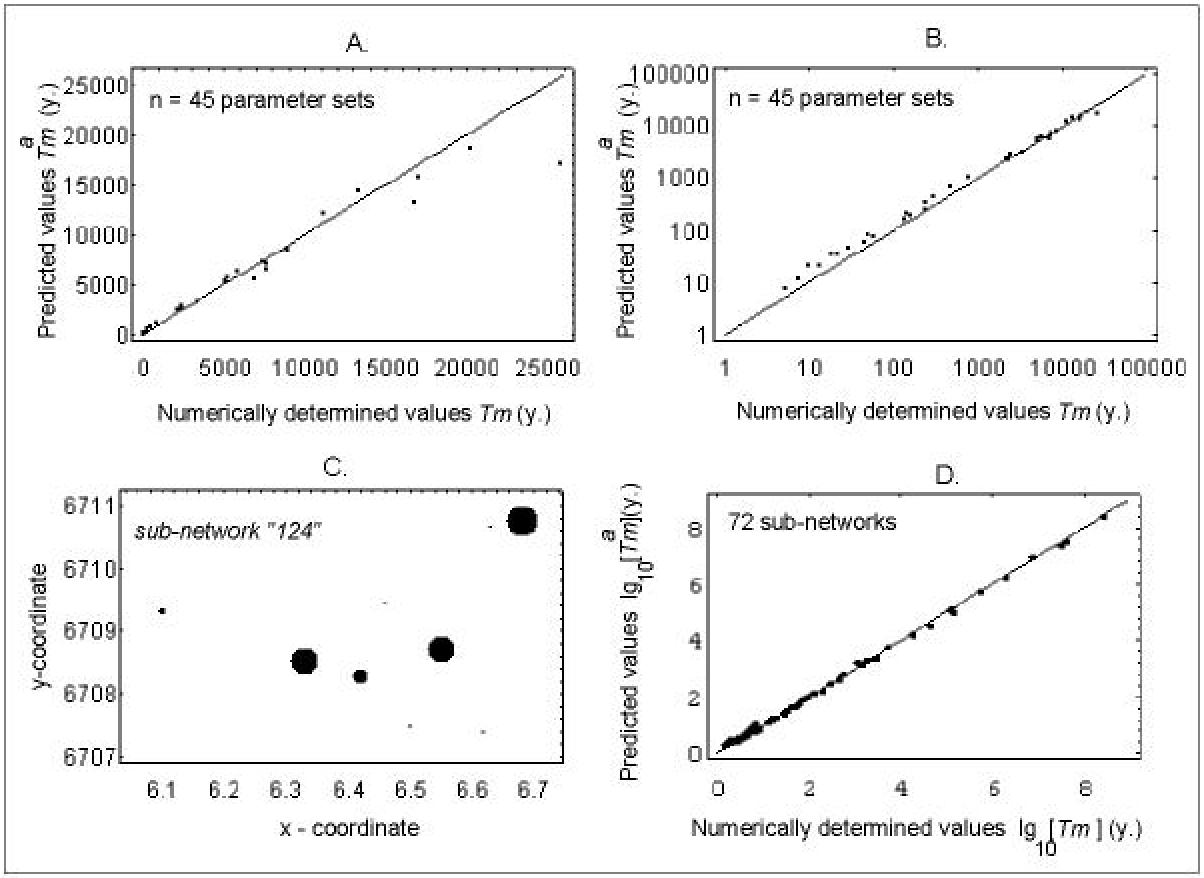

FIGURE 3.6: (A-B) The numerically determined values for the mean lifetime T_m of a metapopulation versus the values predicted with the approximation formula T_m^a (3.20) for all situations described Figs. 3.3C-D and 3.5A-D and patch distances d/d_ρ {0.5, 2, 4}, where (A) shows the absolute values and (B) the double-logarithmic plot. The lines indicate an identity. (C-D) Application of formula T_m^a to 72 sub-networks of the Glanville Fritillary butterfly (*Melitaea cinxia*) system (Hanski *et al.* 1996) on the Åland islands, SW Finland, where (C) shows a particular sub-network and (D) the result of the comparison between numerically determined and predicted values of the mean lifetime for all 72 sub-networks. In this study, the time-continuous version of the Incidence Function Model was taken as a basis ($\nu_i = 0.1\, A_i{}^{-1}$; $\rho_{ij} = 0$; $c_{ij} = 10\, A_i\, e^{-d_{ij}}$).

area (0.002 to 3.8 ha) as well as configuration (for an example, see Fig. 3.6C). In this particular study, a time-continuous version of the Incidence Function Model (see the end of Sec. 3.1.1) was taken as a basis. The result of the comparison between numerically determined and predicted values for the mean lifetime T_m is shown in Fig. 3.6D. The high correspondence between both values corroborates that T_m^a approximates T_m very well. There is also certain evidence for the qualitative reasonableness of formula T_m^a. The functional structure of the aggregated parameters ($\nu_{agg}, (\frac{c_{tot}}{\nu})_{agg}, \rho_{agg}$) reveals that any decrease in the extinction rate ν_i of a certain patch i or the degree of correlation ρ_{ij} of two patches i and j results in a decrease of the corresponding aggregated parameter ν_{agg} (see (3.16)) and ρ_{agg} (see (3.13)) respectively. Furthermore, any increase in the colonization rates c_{ij} from a certain patch i to a certain patch j leads to an increase in $\frac{\mathrm{OUT}(i)}{\nu_i}$ and $\frac{\mathrm{IN}(j)}{\nu_j}$, while the $\frac{\mathrm{OUT}}{\nu}$- and $\frac{\mathrm{IN}}{\nu}$-values of all the other patches remain constant (see (3.18)), with the result that $(\frac{c_{tot}}{\nu})_{agg}$ becomes larger (see (3.17)). All these effects induce an increase in $T_m^a = T_m^{h,a}(N, \nu_{agg}, (\frac{c_{tot}}{\nu})_{agg}, \rho_{agg})$ because of the functional behavior of $T_m^{h,a}$. This shows that the formula for the mean lifetime presented (3.20) allows a number of well-known qualitative effects on metapopulation survival to be correctly reflected.

To summarize, the ability of formula (3.20) to approximate the mean lifetime T_m produced by the model was tested for a wide range of hypothetical as well as real situations with a high variation in the spatial structure of the underlying habitat networks. Different types of dispersal have also been considered (remember the “oriented movement” in the hypothetical studies and the “purely random walk” in the case study). In each case, the results were promising. Moreover, the functional structure of formula T_m^a has been found to reproduce a number of well-known qualitative effects on metapopulation survival. Last but not least, the predictive power of the components of formula (3.20) – the approximation formula $T_m^{h,a}$ for the homogeneous case and the aggregated parameters p_{agg} – was separately tested, with the result that whole functional relationships were qualitatively correctly and quantitatively sufficiently reproduced (Figs. 3.2, 3.3, 3.5). All these arguments indicate that approximation formula T_m^a is really working.

A first analysis of the functional structure of formula T_m^a

The functional structure of approximation formula (3.20) together with formula (3.10) gives rise to numerous consequences for assessing the mean lifetime T_m of quasi-stationary metapopulations: (a) The mean lifetime T_m is always proportional to the aggregated mean lifetime $T_{agg} = \frac{1}{\nu_{agg}}$ of its local populations. This allows T_{agg} to be chosen as the basic time scale of any metapopulation dynamics. The corresponding lifetime ratio T_m/T_{agg} may be used as a quantifier for the survival advantage of the metapopulation over its local populations. This quantity, however, only depends on $(N, (\frac{c_{tot}}{\nu})_{agg}, \rho_{agg})$. (b) If metapopulations of a certain fixed number of patches N without any correlation between the extinction processes ($\rho_{agg} = 0$) are considered, then formula (3.20) together with (3.10; 3.11; 3.12) shows that $T_m^a/T_{agg} \approx \frac{(N-1)!}{N\cdot(N-1)^{N-1}} \cdot ((\frac{c_{tot}}{\nu})_{agg})^{N-1}$. This means that there is exactly one quantity summarizing all the effects relevant to the survival advantage T_m/T_{agg} of a metapopulation: the effective colonization ability $(\frac{c_{tot}}{\nu})_{agg}$ of its local populations.

3.3 An implication: formulas for evaluating habitat networks regarding metapopulation persistence

The approximation formula T_m^a presented also partly answers the question of how to evaluate and compare habitat networks regarding their effect on metapopulation survival. So far, the effect of the habitat network on the survival chance of a given metapopulation was difficult to assess. Even if the effect of the habitat network on the main processes (extinction/recolonization) is well-known, its effect on the long-term dynamics of the metapopulation is hard to predict because of the randomness in the individual processes. This especially impedes a comprehensive understanding of the interaction between all the characteristics of a species and habitat network relevant for metapopulation survival. Yet such an understanding is needed to directly predict the survival chance of a metapopulation on the basis of species and landscape data. The presented formula T_m^a for the mean lifetime of a metapopulation provides a way of overcoming this problem.

Formulas for estimating the survival chance of quasi-stationary metapopulations

The survival chance $S(t)$ of a quasi-stationary metapopulation, i.e. the probability that it is still alive at time t, is given by $S(t) = e^{-t/T_m}$ and so completely determined by the corresponding mean lifetime T_m, as we know from relation (3.6). Since T_m can be approximated by T_m^a (see (3.20)), the following approximation formula for $S(t)$ results:

$$S(t)^a := e^{-t/T_m^a}. \tag{3.21}$$

This relation together with formula T_m^a (3.20) and the aggregation rules (3.13; 3.16; 5.3) reveals how all the relevant data of the species and habitat network have to be combined to estimate the resulting survival chance. This can be achieved by the following procedure:

1. Analyze the habitat network and determine patch size A_i and patch distances d_{ij}.
2. Determine the probability of extinction ν_i and the mean number of emigrants E_i for each local population by statistical analysis or using submodels (e.g., $\nu_i = e \cdot {A_i}^{-x}$, $E_i = \delta \cdot {A_i}^{b}$).
3. Determine the dispersal range d_a and the correlation length d_ρ of the extinction processes.
4. Calculate the degree of correlation ρ_{ij} and the probability of arrival a_{ij} by using (3.2;3.5).
5. Calculate the aggregated parameters $(\nu_{agg}, E_{agg}, a_{agg}, \rho_{agg})$ by using (3.13; 5.3; 3.16).
6. Calculate the approximated lifetime T_m^a by using (3.20) with $(\frac{c_{tot}}{\nu})_{agg} = \frac{E_{agg} \cdot a_{agg}}{\nu_{agg}}$.
7. Calculate the approximated survival chance $S(t)^a$ by using (3.21). If one is merely interested in the relative survival advantage T_m/T_{agg} of a metapopulation over its local populations (Sec. 3.2.2), calculate T_m^a/T_{agg} instead of $S(t)^a$ by using (3.16; 3.20).

All the data concerning the spatial structure of the habitat network needed (e.g., A_i, d_{ij}) can be extracted from landscape maps or Geographical Information Systems (G.I.S.). The determination of the species' ecological parameters (e.g., $e, x, \delta, b, d_a, d_\rho$) is much more difficult. However, there are different ways of attaining a parameterization. Certain parameters can be directly determined in the field or taken from the literature. Another possibility is indirect determination by using parameter estimation techniques (see Hanski 1994; Moilanen 1999). If one is only interested in the relative importance of a certain factor for metapopulation survival, it suffices to have rough estimations for the relevant parameters (worst case - best case; lower limit - upper limit).

Currencies for ranking habitat networks according to their effect on persistence

All formulas T_m^a, T_m^a/T_{agg}, and $S(t)^a$ give a single scalar value as a result of the habitat network evaluation. Hence, they provide an ecological "currency" for evaluating, comparing and ranking all habitat networks according to their effect on metapopulation persistence, even if these networks are structurally dissimilar. These currencies take both the spatial structure of a habitat network and the species' specific response to it into account. This fact is one of the most important consequences of the presented formula T_m^a.

If all the habitat networks under consideration have the same number of patches N and a negligible correlation between the extinction processes ($\rho_{agg} \approx 0$), and one is only interested in the survival advantage T_m/T_{agg} of the corresponding metapopulations over their local populations, a much simpler currency for ranking these networks can be provided. Remember that the effective colonization ability $(\frac{c_{tot}}{\nu})_{agg}$ of the local populations has been found to summarize all the important effects on T_m/T_{agg} (end of Sec. 3.2.2.2). Therefore, it suffices to analyze $(\frac{c_{tot}}{\nu})_{agg}$ in order to rank the habitat networks according to their effect on T_m/T_{agg} (the resulting ranking orders will be the same). To demonstrate the advantage of using $(\frac{c_{tot}}{\nu})_{agg}$ instead of T_m^a/T_{agg} itself, we take the same submodels ($\nu_i = e \cdot {A_i}^{-x}$; $E_i = \delta \cdot {A_i}^{b}$) for including patch area A_i as in the Incidence Function Model (Hanski 1994) as the basis and show how $(\frac{c_{tot}}{\nu})_{agg}$ looks like in this particular case. When inserting the specified parameters (ν_i, E_i) in the formula (3.17) for $(\frac{c_{tot}}{\nu})_{agg}$, we get

$$\left(\frac{c_{tot}}{\nu}\right)_{agg} = \sqrt{2} \cdot \frac{\delta}{e} \cdot \prod_{i=1}^{M} \sqrt{\frac{{A_i}^{2x}}{(\sum_{j(\neq i)} {A_i}^{b} \cdot e^{-d_{ij}/d_a})^{-2} + (\sum_{j(\neq i)} {A_j}^{b} \cdot e^{-d_{ji}/d_a})^{-2}}}^{\frac{1}{N}} . \tag{3.22}$$

This formula is much simpler than the formula T_m^a/T_{agg} for the survival advantage T_m/T_{agg} itself. This provides an extra benefit: insight into the interplay between spatial structure (A_i, d_{ij}) and species' ecology (e, x, δ, d_a) and the effect on metapopulation persistence.

To summarize, by taking the presented approximation formula T_m^a as a basis, a set of formulas ($S(t)^a$, T_m^a/T_{agg}, $(\frac{c_{tot}}{\nu})_{agg}$) was extracted for estimating the persistence of a metapopulation as well as evaluating and comparing habitat networks from different perspectives of metapopulation survival. This mainly resulted from the fact that T_m^a includes aggregated parameters that summarize the whole spatial complexity of established metapopulations. But note that all these formulas can only be as good as the underlying model regarding the effects on metapopulation survival that can be reflected. This means that the findings may change if additional aspects (e.g. rescue effects) are taken into account by the model.

3.4 Discussion

3.4.1 Two reasons for the successful deduction of an approximation formula for the mean lifetime of metapopulations

Although the considered spatially realistic metapopulation model (Chapter 2) is complex due to heterogeneity, an approximation formula T_m^a for the mean lifetime T_m of (quasi-stationary) metapopulations in heterogeneous landscapes was deduced. This success can be mainly attributed to the following two facts:

3.4.1.1 A non-spatial model was found to reproduce the behavior of the considered spatially realistic one

One of the most important results of the present paper is the finding that the parameters p_i (p_i stands for ν_i, E_i, a_{ij}, ρ_{ij}) of the underlying model can be aggregated such that the homogeneous version of this model applied to the aggregated parameters p_{agg} gives nearly the same mean lifetime T_m of a quasi-stationary metapopulation as the original one, i.e. $T_m^h(p_{agg}) \approx T_m(p_i)$. This means that a simple non-spatial model already allows all the effects on the mean lifetime T_m covered by the spatially realistic model to be reproduced, provided its parameters p are appropriately specified ($p = p_{agg}$). The whole spatial complexity is summarized in the aggregated parameters p_{agg}. This underlines the outstanding importance of knowing the right aggregation rules. The aggregation rules presented (3.13; 5.3; 3.16; 3.17) therefore provide some "instructions" for correctly applying the non-spatial model to heterogeneous landscapes.

3.4.1.2 An approximation formula $T_m^{h,a}$ was deduced for the non-spatial model

This deduction was only possible because, in the special case of uncorrelated circumstances, an exact formula T_m^{GoRi} (see (3.7)) for the mean lifetime of initially completely occupied metapopulations was available, that approximates the mean lifetime $T_m^{h,u}$ of quasi-stationary metapopulations. When turning from the exact formula T_m^{GoRi} to its analytically determined approximation (see (3.8)), the essential functional structure of $T_m^{h,u}$

came to light (here: a power-like relationship between $(\nu \cdot T_m^{h,u} \cdot e^{-\frac{N}{c_{tot}/\nu}})$ and $\frac{c_{tot}}{\nu}$). This structure gave some idea of how to proceed with the mean lifetime T_m^h in the general homogeneous case where T_m^h can only be numerically determined. By non-linear regression, the same power-like relationship was found and the corresponding power and pre-factor were determined. Hence, by combining analytical and numerical techniques, the essential functional structure of T_m^h could be uncovered.

The desired approximation formula T_m^a for the heterogeneous case finally resulted from applying approximation formula $T_m^{h,a}$ to the aggregated parameters p_{agg}, i.e. $T_m^a := T_m^{h,a}(p_{agg})$. This shows that the knowledge of both components, $T_m^{h,a}$ and p_{agg}, is essential. Whenever the functional structure of one component would have been unknown, the whole project of deriving an approximation formula for the mean lifetime T_m would have failed. But note that the formula T_m^a presented is only valid for quasi-stationary metapopulations. In the case of transient metapopulations, the functional structure of T_m may be different.

The presented formula T_m^a provides a number of features which are helpful for assessing metapopulation persistence (Sec. 3.4.2). Its main advantage, however, is the disclosure of the complete functional relationship between mean lifetime T_m and the model parameters. It can now be simply “read off” how landscape and species ecological factors interact and influence each other in their effect on the metapopulation level. Merely by analyzing the functional structure of T_m^a, we were able to derive formulas for comparing dissimilar habitat networks regarding their ecological effect (Sec. 3.3). This opens up new perspectives for analyzing the role of spatial heterogeneity in interplay with stochasticity for metapopulation persistence. But note that the functional structure of T_m^a is a reflection of the structure of the underlying model. This means that a change in the model structure (e.g. by including additional mechanisms) may result in an altered structure of T_m^a.

3.4.2 The practical value of approximation formula T_m^a

The approximation formula T_m^a for the mean lifetime of metapopulations presented also has some practical value, especially for the field of metapopulation conservation.

It is well-known that mathematical models can multifariously support decision-making in conservation management. PVA models, for instance, allow the persistence of a population to be estimated (Akçakaya and Ferson 1990). Alternative management activities can be simulated as special parameter changes (Lankester *et al.* 1991; Stelter *et al.* 1997) and compared in terms of their effect on the persistence of the target population. The only problem is that a decision-maker will seldom have the possibility to develop PVA models himself. Moreover, models will only have some practical value for him if an implementation, i.e. an appropriate computer program, is available as well. Last but not least, helpful results can only be attained if the right model experiments are performed, i.e. the right quantities are related to each other. This requires plenty of experience in working with models, running and evaluating simulations or solving model equations.

As the present study demonstrates, there is an alternative to utilizing computer programs for metapopulation viability analysis, such as RAMAS (Akçakaya and Ferson 1990), VORTEX (Lacy 1993), ALEX (Possingham and Davies 1995; Lindenmayer *et al.* 1995), or META-X (Frank *et al.* 2002). If formulas for the mean lifetime T_m or the probability of extinction $P_0(t)$ are available, then a complete population viability analysis can be performed without having to run any simulation. Since the approximation formula T_m^a for the mean lifetime presented, for instance, is based on the same model as META-X, formula and software predict the same values for T_m and, hence, give rise to the same conclusions for metapopulation management. The advantage of formulas is that, once disclosed, they can immediately be used for the viability analysis. Hence, the decision-maker is no longer dependent on the availability of a computer program. The extraction of such formulas undoubtedly requires much model analysis work. But this work can be kept away from the user and undertaken by the modeler himself, who anyway knows the model best.

3.4.3 Aggregation as bridging technique between complex spatially realistic and simple models

One of the main topics of recent Theoretical Ecology is the methodology of modeling spatiotemporal dynamics in ecological systems (e.g., Durrett and Levin 1994; Bascompte and Solé 1998). Two questions are of particular importance: “What degree of detail is needed to reflect all the important effects of space?", and "Are there any ways of reducing the complexity of spatially realistic models and finding a bridge to simpler models?". Techniques such as pair approximation (Matsuda *et al.* 1992; Sato *et al.* 1994) and moment closure (Bolker and Pacala 1997; Law and Dieckmann 1998) are widely discussed in this context. The present study shows that aggregation also provides a promising technique of model simplification. Aggregation-based methods are very common in physics, especially in the fields of thermodynamics and statistical physics (e.g., Dickman 1986; Uzunov 1993; Pitaevskii 1999) as well as condensed matter physics and magnetism (e.g., Fujimoto 1997; Schroeder 2000; Majlis 2001). But these methods have so far only rarely been used in ecology (e.g., Bascompte 2001). We therefore take our model results as the basis and draw some conclusions concerning both the benefits of using aggregation techniques in the field of (meta-)population modeling and the possibility of extending the methods presented to other ecological situations. Finally, the potential of aggregation for the derivation of measures for landscape evaluation through the eyes of a certain species is discussed.

3.4.3.1 The benefits of aggregation techniques

As we have seen, a simple non-spatial model is able to give the same mean lifetime of an quasi-stationary metapopulation as the spatially realistic model considered (i.e. $T_m^h \approx T_m$), provided it is applied to appropriate aggregations p_{agg} of the parameters p_i of the original model. To answer a certain question concerning metapopulation persistence, it therefore suffices to analyze the non-spatial model and to extend the results to spatially realistic situations by using the aggregated parameters p_{agg}. This was precisely what was done when deducing the approximation formula T_m^a for the mean lifetime ($T_m^a(p_i) := T_m^{h,a}(p_{agg})$). The aggregation formulas reveal how the interplay between the local populations influences the persistence of the whole metapopulation. This shows that aggregation-based model simplifications allow spatial realism and simplicity to be combined to the benefit of better understanding. This advantage especially comes to fruition when the model takes the interplay between species and landscape into account.

3.4.3.2 Aggregation as an approach to ecologically scaled landscape indices

In the case that aggregation techniques are successfully used for deriving an approximation formula Q^a for a certain target quantity Q of a certain spatial (meta-)population model, an extra-benefit can be provided. The resulting approximation formula Q^a reveals how data from species and landscape have to be combined to estimate the value for the target quantity Q of interest. Therefore, Q^a(landscape, species) provides a measure that allows a given landscape to be evaluated through the eyes of a certain species. This aggregation-based approach towards ecologically scaled landscape indices goes in the same direction as the approaches of Wiegand *et al.* (1999) and Vos et al. (2001), each utilizing a spatially realistic (meta-)population model to link landscape structure with population dynamical processes. A comparative analysis of the different approaches concerning their range of applicability, benefits and limitations will be presented in Chapter 9 of this thesis.

3.4.4 Prospects for further research

In this study, we developed a method for deducing a formula for the mean lifetime T_m of metapopulations in heterogeneous landscapes. To demonstrate its potential, it was applied to a model which belongs to the widely used class of Levins-type metapopulation models. The simplifying assumptions underlying this study indicate some prospects for further research. (a) The applicability of both the presented aggregation rules (3.13; 3.16; 3.17) and the final approximation formula (3.20) ought to be tested in situations where the rescue effect is taken into account or the functional forms for arrival probability and correlation are more sophisticated. (b) Approximation formulas ought also to be deduced for other target quantities of interest in the metapopulation context such as the mean lifetime $T_m(\underline{x}_0)$ of a transient metapopulation or the probability $R(\underline{x}_0)$ that a metapopulation successfully approaches quasi-stationarity (Goel and Richter-Dyn 1974; Wissel *et al.* 1994) where $\underline{x}_0$ denotes the initial state. Both quantities are important for questions concerning the recovery or foundation of metapopulations. (c) As we already mentioned in Sec. 4, there is a strong structural relationship between the effective colonization ability of the local populations $(\frac{c_{tot}}{\nu})_{agg}$ given in relation (3.22) and the metapopulation capacity

λ_M defined by Hanski and Ovaskainen (2000). Both quantities provide a landscape measure for metapopulation persistence - the first a stochastic and the second a deterministic one. In a forthcoming paper, both measures will be compared to the benefit of a better understanding of the effect of stochasticity on metapopulation survival.

3.5 Appendix

3.5.1 Analytical approximation of the Goel and Richter-Dyn formula T_m^{GoRi}

In the following, the exact formula T_m^{GoRi} (see (3.7)) for the mean lifetime of an initially completely occupied, uncorrelated, homogeneous metapopulation is analytically approximated for values of $\frac{c_{tot}}{\nu} > 5$. By setting $x = \frac{c_{tot}}{\nu}$, formula (3.7) is transformed into

$$\begin{aligned} T_m^{GoRi} &= \tfrac{1}{\nu} \cdot \sum_{i=1}^{N} \sum_{k=i}^{N} \tfrac{1}{k} \cdot \tfrac{(N-i)!}{(N-k)!} \cdot \tfrac{1}{(N-1)^{k-i}} \cdot x^{k-i} \\ &\overset{m=N-k}{=} \tfrac{1}{\nu} \cdot \sum_{i=1}^{N} \sum_{m=0}^{N-i} \tfrac{1}{N-m} \cdot \tfrac{(N-i)!}{m!} \cdot \tfrac{1}{(N-1)^{N-i-m}} \cdot x^{N-i-m} \qquad (3.23) \\ &= \tfrac{1}{\nu} \cdot \sum_{i=1}^{N} \left(\sum_{m=0}^{N-i} \tfrac{1}{N-m} \cdot \tfrac{1}{m!} \cdot (\tfrac{N-1}{x})^m \right) \cdot \tfrac{(N-i)!}{(N-1)^{N-i}} \cdot x^{N-i} \end{aligned}$$

This relation reveals that T_m^{GoRi} is a polynomial in x of degree $N-1$. For larger values of x, T_m^{GoRi} can be approximated by its dominant part given by the summand related to x^{N-1} that can be found at position $i = 1$ of the last sum in relation (3.23). Therefore

$$\begin{aligned} \text{dominant part of } T_m^{GoRi} &= \tfrac{1}{\nu} \cdot \left(\sum_{m=0}^{N-1} \tfrac{1}{N-m} \cdot \tfrac{1}{m!} \cdot (\tfrac{N-1}{x})^m \right) \cdot \tfrac{(N-1)!}{(N-1)^{N-1}} \cdot x^{N-1} \\ &= \tfrac{1}{\nu} \cdot \left(\sum_{m=0}^{N-1} \tfrac{N}{N-m} \cdot \tfrac{1}{m!} \cdot (\tfrac{N-1}{x})^m \right) \cdot \tfrac{(N-1)!}{N \cdot (N-1)^{N-1}} \cdot x^{N-1}. \qquad (3.24) \end{aligned}$$

Figure 3.7 indicates that the term in parentheses can be approximated by $e^{N/x}$ as long as $x > 2.5$ and $N \geq 5$. This results in the following approximation for T_m^{GoRi}:

$$T_m^{GoRi} \approx \tfrac{1}{\nu} \cdot e^{N/x} \cdot \tfrac{(N-1)!}{N \cdot (N-1)^{N-1}} \cdot x^{N-1} \qquad (3.25)$$

provided $x > 2.5$ and $N \geq 5$. Finally, if the term x in (3.25) is replaced by the expression $\frac{c_{tot}}{\nu}$, then we get the same functional relationship as mentioned in relation (3.8).

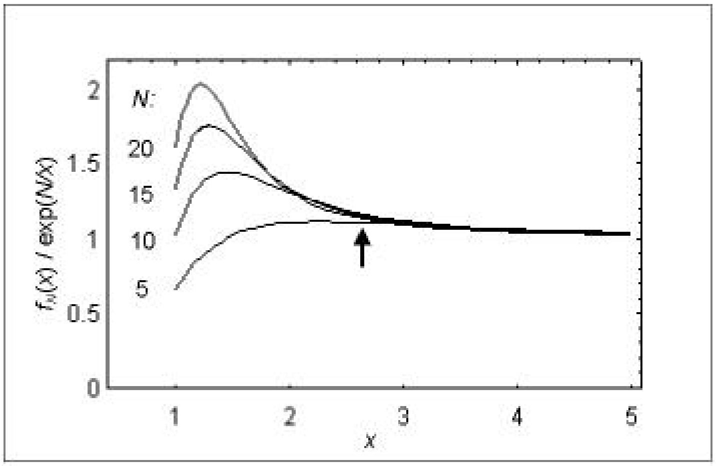

FIGURE 3.7: Ratio $f_N(x)/\exp(N/x)$ of the functions $f_N(x) := \sum_{m=0}^{N-1} \frac{N}{N-m} \cdot \frac{1}{m!} \cdot (\frac{N-1}{x})^m$ and $\exp(N/x)$ versus x for different natural numbers N. The ratio is found to be ≈ 1 for $x > 2.5$ and $N \geq 5$ (see arrow). Hence, $\exp(N/x)$ gives a good approximation of $f_N(x)$ in this region.

3.5.2 Calculations indicating a saturation behavior of E_{agg}

In the following, we show that the aggregation E_{agg} of the numbers of emigrants E_i given in (5.3) converges to the limit value $\sqrt{2} \cdot (\frac{N-1}{\sum_{n(\neq 1)} a_{n1}})^{\frac{1}{N}} \cdot (\mathrm{IN}(1) \cdot \prod_{i(\neq 1)} E_i)^{\frac{1}{N}}$ if the value E_1 for patch 1 becomes very large, where IN(1) denotes the total recolonization chance of patch 1, $\sum_{j(\neq 1)} \frac{E_j}{N-1} a_{j1}$. Since $(\frac{1}{x} + \frac{1}{a})^{-1}$ converges to a if x becomes large, we get:

$$\begin{aligned} E_{agg} &= \prod_{i=1}^{N} \sqrt{\left(\frac{1}{2}\left(\frac{1}{{E_i}^2} + \frac{1}{(\sum_{j(\neq i)} w_j^i\, E_j)^2}\right)\right)^{-1}}^{\frac{1}{N}} \qquad (3.26) \\ &= \sqrt{2} \cdot \underbrace{\sqrt{\left(\frac{1}{{E_1}^2} + \frac{1}{(\sum_{j(\neq 1)} w_j^1\, E_j)^2}\right)^{-1}}^{\frac{1}{N}}}_{\overset{E_1\to\infty}{\longrightarrow} \sqrt{(\sum_{j(\neq 1)} w_j^1\, E_j)^2}} \\ &\quad \times \prod_{i(\neq 1)} \underbrace{\sqrt{\left(\frac{1}{{E_i}^2} + \frac{1}{(w_1^i\, E_1 + \sum_{j(\neq i,1)} w_j^i\, E_j)^2}\right)^{-1}}^{\frac{1}{N}}}_{\overset{E_1\to\infty}{\longrightarrow} \sqrt{{E_i}^2}} \end{aligned}$$

Since the weights w_j^i in (3.26) are defined to be $a_{ji}/\sum_{n(\neq i)} a_{ni}$ (see (3.15)), we obtain

$$\lim_{E_1\to\infty} E_{agg} = \sqrt{2}\cdot\left(\frac{N-1}{\sum_{n(\neq 1)} a_{n1}}\right)^{\frac{1}{N}} \cdot \underbrace{\left(\sum_{j(\neq 1)} \frac{E_j}{N-1}\, a_{j1}\right)^{\frac{1}{N}}}_{\text{IN}(1)} \cdot \prod_{i(\neq 1)} E_i^{\frac{1}{N}} \tag{3.27}$$

This shows that the aggregated parameter E_{agg} converges to the limit value mentioned.

3.5.3 Analysis of the functional structure of $(\frac{c_{tot}}{\nu})_{agg}$

To finalize, we calculate the term $(\frac{c_{tot}}{\nu})_{agg} = \frac{E_{agg}\cdot a_{agg}}{\nu_{agg}}$ by using the presented formulas (3.13; 5.3; 3.16) for the aggregated parameters $(\nu_{agg}, E_{agg}, a_{agg})$. It is obvious that

$$\begin{aligned}
\frac{E_{agg}\cdot a_{agg}}{\nu_{agg}} &= \prod_{i=1}^{N}\left(\frac{1}{\nu_i}\cdot\sqrt{\left(\frac{1}{2}\left(\frac{1}{{E_i}^2}+\frac{1}{(\sum_{j(\neq i)} w_j^i\, E_j)^2}\right)\right)^{-1}}\cdot\frac{1}{N-1}\sum_{n(\neq i)} a_{ni}\right)^{\frac{1}{N}} \\
&= \prod_{i=1}^{N}\left(\frac{1}{\nu_i}\cdot\sqrt{\left(\frac{1}{2}\left(\frac{1}{(\sum_{n(\neq i)}\frac{E_i}{N-1}\,a_{ni})^2}+\frac{1}{(\sum_{j(\neq i)}\frac{E_j}{N-1}\,a_{ji})^2}\right)\right)^{-1}}\right)^{\frac{1}{N}} \\
&\overset{a_{ni}=a_{in}}{=} \prod_{i=1}^{N}\left(\frac{1}{\nu_i}\cdot\sqrt{\left(\frac{1}{2}\left(\frac{1}{(\sum_{n(\neq i)} c_{in})^2}+\frac{1}{(\sum_{j(\neq i)} c_{ji})^2}\right)\right)^{-1}}\right)^{\frac{1}{N}}.
\end{aligned} \tag{3.28}$$

This shows that $(\frac{c_{tot}}{\nu})_{agg} = \prod_{i=1}^{N}\sqrt{2/\left((\frac{\text{OUT}(i)}{\nu_i})^{-2}+(\frac{\text{IN}(i)}{\nu_i})^{-2}\right)}^{\frac{1}{N}}$ as stated in relation (3.17).

3.6 References

Adler, F. R., and B. Nuernberger. 1994. Persistence in patchy irregular landscapes. Theoretical Population Biology 45: 41–75

Anderson, W.J. 1991. Continuous Time Markov Chains. Springer-Verlag, New York

Anderson, R. A., and R. M. May 1991. Infectious Diseases of Humans - Dynamics and Control. Oxford University Press, Oxford

Akçakaya, H. R., and S. Ferson. 1990. RAMAS - Spatially Structured Population Models for Conservation Biology. Applied Biomathematics. Setauket, New York

Akçakaya, H. R., and J. L. Atwood. 1997. A habitat-based metapopulation model of the California Gnatcatcher. Conservation Biology 11: 422–434

Baars, M. A., and T. H. van Dijk. 1984. Population dynamics of carabid beetles at a Dutch heathland. I. Subpopulation fluctuations in relation to weather and dispersal. Journal of Animal Ecology 53: 375–388

Bascompte, J., and R. V. Solé, eds. 1998. Modeling Spatiotemporal Dynamics in Ecology. Springer-Verlag, Berlin

Bascompte, J. 2001. Aggregate statistical measures and metapopulation dynamics. Journal of Theoretical Biology (in press)

Bolker, B., and S. W. Pacala. 1997. Using moment equations to understand stochastically driven spatial pattern formation in ecological systems. Theoretical Population Biology 52: 179–197

Boyce, M.S. 1992. Population viability analysis. Ann. Rev. Ecol. Systematics. 23: 481–506

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58: 445–449

Burgman, M.A., Ferson, S., and Akçakaya, H.R. 1993. Risk assessment in conservation biology. Chapman and Hall, London

Day, J. R., and H. P. Possingham. 1995. A stochastic metapopulation model with variability in patch size and position. Theoretical Population Biology 48: 333-360

Dickman, R. (1986). Kinetic phase transitions in a surface-reaction model: mean-field theory. Physical Reviews A 34: 4246–4250

Doak, D. F., P. C. Marino, and P. M. Kareiva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. Theoretical Population Biology 41: 315–336

Durrett, R., and S. Levin. 1994. Stochastic spatial models: a user's guide to ecological applications. Philosophical Transactions of the Royal Society London B 343: 329–350

Drechsler, M., and C. Wissel. 1997. Separability of local and regional dynamics in metapopulations. Theoretical Population Biology 51: 9–21

Etienne, R.S., and Heesterbeek, J.A.P. 2001. Rules of thumb for conservation of metapopulations based on a stochastic winking-patch model. *The American Naturalist* 158: 389-407

Fahrig, L. 1992. Relative importance of spatial and temporal scales in a patchy environment. Theoretical Population Biology 41: 300–314

Fahse, L., C. Wissel, and V. Grimm. 1998. Reconciling classical and individual-based approaches of theoretical population ecology: a protocol to extract population parameters from individual-based models. The American Naturalist 152: 838–852

Foley, P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. Conservation Biology 8: 124-137

Frank, K., and C. Wissel. 1994. Ein Modell über den Einfluß räumlicher Aspekte auf das Überleben von Metapopulationen. Verhandlungen der Gesellschaft für Ökologie 23: 303–310

Frank, K., and C. Wissel. 1998. Spatial aspects of metapopulation survival: from model results to rules of thumb for landscape management. Landscape Ecology 13: 363-379

Frank, K., H. Lorek, M. Sonnenschein, C. Wissel, and V. Grimm. 2001. META-X: Software for Metapopulation Viability Analysis. Springer-Verlag, Berlin

Fujimoto, M. 1997. The Physics of Structural Phase Transitions. Springer-Verlag, New York

Gilpin, M. E. 1990. Extinction of finite metapopulations in correlated environments. Pages 177–186 in B. Shorrocks, ed. Living in a Patchy Environment. Oxford University Press, Oxford

Gilpin, M. E. 1991. The effective size of metapopulations. Biological Journal of the Linnean Society 42: 165–175

Goel, N. S., and N. Richter-Dyn. 1974. Stochastic Models in Biology. Academic Press, New York

Gyllenberg, M., and D. Silvestrov. 1994. Quasi-stationary distributions of a stochastic metapopulation. Journal of Mathematical Biology 33: 35–70

Hanski, I. 1989. Metapopulation dynamics: Does it help to have more of the same? Trends in Evolution and Ecology 4: 113–114

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63: 151–163

Hanski, I. 1998. Metapopulation dynamics. Nature 396: 41–49

Hanski, I. 1999. Metapopulation Ecology. Oxford University Press, Oxford

Hanski, I., and M. E. Gilpin. 1997. Metapopulation Biology: Ecology, Genetics, and Evolution, Academic Press, San Diego

Hanski, I., A. Moilanen, T. Pakkala, and M. Kuussaari. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. Conservation Biology 10: 578–590

Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. Nature 404: 755-758

Hanski, I., and I. P. Woiwod. 1993. Spatial synchrony in the dynamics of moth and aphid populations. Journal of Animal Ecology 62: 656–504

Harrison, S., D. D. Murphy, and P. R. Ehrlich. 1988. Distribution of the Bay Checkerspot butterfly, *Euphrydyas editha bayensis*: evidence for a metapopulation model. The American Naturalist 132: 360–382

Harrison, S., and J. F. Quinn. 1989. Correlated environments and the persistence of metapopulations. Oikos 56: 1–6

Lacy, R. C. 1993. VORTEX - a model for use in population viability analysis. Wildlife Research 20: 45–65

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. The American Naturalist 142: 911-927

Lande, R., and G. F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. Pages 87–123 in M.E. Soule, ed. Viable Populations for Conservation. Cambridge University Press, Cambridge

Lankester, K., R. van Apeldoorn, E. Meelis, and J. Verboom. 1991. Management perspectives for populations of the Eurasian badger (*Meles meles*) in a fragmented landscape. Journal of Applied Ecology 28: 561–573

Law, R., and U. Dieckmann. 1998. On scaling up from individual-based processes to macroscopic ecological dynamics in spatially-extended communities. Interim Report IR-98-046 of the IIASA

Leigh, E. G. 1981. The average lifetime of a population in a varying environment. Journal of Theoretical Biology 90: 213–239

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15: 237–240

Lindenmayer, D. B., M. A. Burgman, H. R. Akcakaya, R. C. Lacy, and H. Possingham. 1995. A review of the generic computer programs ALEX, RAMAS/space and VORTEX for modeling the viability of wildlife metapopulations. Ecological Modeling 82:161–174

Majlis, N. 2001. The Quantum Theory of Magnetism. World Scientific Publishing Company, Singapore

Matsuda, H., N. Ogita, A. Sasaki, and K. Sato. 1992. Statistical mechanics of population - the lattice Lotka-Volterra model. Progress in Theoretical Physics 88: 1035–1049

Middleton, D. A. J., and R. M. Nisbet. 1997. Population persistence time: estimates, models, and mechanisms. Ecological Applications 7: 107–117

Moilanen, A. 1999. Patch occupancy models of metapopulation dynamics: efficient parameter estimation using implicit statistical inference. Ecology 80: 1031–1043

Moilanen, A., A. T. Smith, and I. Hanski. 1998. Long-term dynamics in a metapopulation of American pika. The American Naturalist 152: 530–542

Moloney, K. A. 1993. Determining process through pattern: reality or fantasy. Pages 61–69 in: S. A. Levin, T. M. Powell, and J. H. Steele, eds. Patch-Dynamics (Lecture Notes in Biomathematics 96), Springer-Verlag, Berlin

Nisbet, R. M., and W. S. C. Gurney. 1982. Modelling fluctuating populations. John Wiley & Sons, New York

Ovaskainen, O. and Hanski, I. 2004. Metapopulation dynamics in highly fragmented landscapes. in I. Hanski, and O. Gaggiotti (eds.) Ecology, Genetics, and Evolution in Metapopulations, Academic Press, pp. 73-103

Pitaevskii, L. P. 1999. Trapped Bose gas: mean field approximation and beyond. International Journal of Modern Physics B 13: 427–445

Possingham, H. P. and I. Davies. 1995. ALEX: A population viability analysis model for spatially structured populations. Biological Conservation 73:143–150

Possingham, H.P., Lindenmayer, D.B., Norton, T.W., and Davies, I. 1994. Metapopulation viability analysis of the Greater Glider, *Petauroides volans*, in a wood production area. Biological Conservation 70: 227–236

Pulliam, R. E. 1988. Sources, sinks and population regulation. The American Naturalist 132: 652–661

Quinn, J. F., and A. Hastings. 1987. Extinction in subdivided habitats. Conservation Biology 1: 198–208

Sato, K., H. Matsuda, and A. Sasaki. 1994. Pathogen invasion and host extinction in lattice structured populations. Journal of Mathematical Biology 32: 251–268

Schroeder, D. V. 2000. An Introduction to Thermal Physics. Addison-Wesley Publishing Company, New York

Settele, J., C. R. Margules, P. Poschlod, and K. Henle, eds. 1996. Species Survival in Fragmented Landscapes. Kluwer, Dordrecht

Stelter, C., M. Reich, V. Grimm, and C. Wissel. 1997. Modelling persistence in dynamic landscapes: lessons from a metapopulation of grasshopper *Bryodema tuberculata*. Journal of Animal Ecology 66: 508–518

Sutcliffe, O. L., C. D. Thomas, and D. Moss. 1996. Spatial synchrony and asynchrony in butterfly population dynamics. Journal of Animal Ecology 65: 85–95

Tischendorf, L., and C. Wissel. 1997. Corridors as conduits for small animals: attainable distances depending on movement pattern, boundary reaction and corridor width. OIKOS 79: 603–611

Uzunov, D. I. 1993. Introduction to the Theory of Critical Phenomena: Mean Field, Fluctuations and Renormalization. World Scientific Publishing Company, River Edge

Verboom, J., K. Lankester, and J. A. J. Metz. 1991. Linking local and regional dynamics in stochastic metapopulation models. Biological Journal of Linnean Society 42: 39–55

Vos, C. C., and P. Opdam, eds. 1993. Landscape Ecology in a Stressed Environment. Chapman and Hall, London

Vos, C. C., J. Verboom, P. F. M. Opdam, and C. J. F. Ter Braak. 2001. Toward ecologically scaled landscape indices. The American Naturalist 157: 24–41

Wiegand, T., K. A. Moloney, J. Naves, and F.Knauer. 1999 Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. The American Naturalist 154: 605–627

Wissel, C., and S. Stöcker. 1991. Extinction of populations by random influences Theoretical Population Biology 39: 315–328

Wissel, C., Th. Stephan, and S.-H. Zaschke. 1994. Modelling extinction of small populations. Pages 67–103 in H. Remmert, ed. Minimum viable populations. (Ecol. Studies 106)

Wissel, C., and S.-H. Zaschke. 1994. Stochastic birth and death processes describing minimum viable populations. Ecological Modelling 75/76: 193–201

Wolfenbarger, D. O. 1946. Dispersion of small organism. The American Midland Naturalist 35: 1–152

Wolfram, S. 1992. Mathematica: A System for Doing Mathematics by Computer. Addison-Wesley Publishing Company, New York

Wright, S. 1938. Size of population and breeding structure in relation to evolution. Science 87: 430–431

Chapter 4

Minimum conditions for long-term metapopulation persistence

This chapter is mainly based on the following publication:

Frank, K. & Wissel, C. 1998. Spatial aspects of metapopulation survival: from model results to rules of thumb for landscape management. *Landscape Ecology* 13: 363–379

In the preceding two chapters, a stochastic modeling framework for analyses of metapopulation persistence has been developed and an approximation formula for the mean lifetime T_m^a for supplementary, more structural analyses as well. Now the basis is provided for passing on to answering the ecological questions we are interested in.

The main object of research in this thesis is the functional relationship between metapopulation persistence, the landscape structure and the species' ecology. There are numerous spatial factors influencing the metapopulation processes. Some of them are related to the spatial structure of the underlying habitat network such as the number, size, shape and quality of the patches or the scale and relative arrangement of the patch configuration. Other spatial factors are related to the species' ecology such as the correlation length of the extinction processes or the dispersal range. Therefore, it is worth to analyze the relative importance of the individual spatial factors and its dependence on the other factors. From the theoretical point of view, this is interesting because it clarifies the complex spatial effects on metapopulation persistence. From the conservational point of view, this is even more urgent. To have information about the relative importance of a certain spatial factor enables to decision maker to answer the following question: “Is it possible to obtain long-term metapopulation persistence through a controlled change in the factor considered or is it better to change another factor?”. This is an indispensable basis for setting correct management priorities and obtaining efficiency. A topic of particular relevance is the relative importance of the patch configuration because this topic is closely related to the efficiency of reserve network design and habitat connecting.

The relative importance of the patch configuration for metapopulation persistence has been analyzed in several studies. Some studies, however, do not take stochasticity into account (e.g. Doak et al. 1992; Adler and Nuernberger 1994; Hanski and Ovaskainen 2000; Ovaskainen and Hanski 2001). Others ignore the correlation of the extinction processes (e.g. Lefkovitch and Fahrig 1985; Fahrig and Merriam 1985; Hanski 1994). Most studies which take the correlation into account (e.g. Harrison and Quinn 1989; Gilpin 1990; Etienne 2002; Ovaskainen 2003) deal with spatial homogeneity. Sometimes, however, the correlation has a limited range and disappears on a larger scale (Moloney 1993). Akçakaya and Ginzburg (1991) used distance-dependent correlations but considered only systems with two and three patches. Usually, the dispersal strategy was fixed.

In this chapter, we assess the relative importance of the patch configuration for metapopulation persistence, by taking the spatial correlation of the extinction processes into account. We determine species-ecological and landscape-structural conditions which have to be met before the patch configuration can become an actual key factor of metapopulation persistence. Additionally, we provide conditions to be met by the patch configurations themselves to allow long-term metapopulation persistence. We show that (a) the species’ dispersal range d_a has to exceed the correlation length d_ρ before a metapopulation can benefit from changes in the patch configuration at all, (b) long-term persistence can only be obtained if no patch is inside the correlation range of another one, and (c) there is a hierarchy of importance in the characteristics of a patch configuration (scale and relative arrangement) and, hence, in the scopes of landscape management. By taking the scientific results as a basis, we derive rules of thumb for landscape management. These rules qualify and modify the well-known rules for reserve network design by Wilson and

Willis (1975). We finish with remarks on the limitations of supporting species survival by landscape management and draw some conclusions for ecological research.

4.1 Methods

The present study aims at the determination of minimum conditions to be met by species and habitat network to allow long-term metapopulation persistence. This requires systematic analyses of the functional relationship between metapopulation persistence, the species' ecology and the spatial structure of habitat networks (local attribtes, patch configuration). A subdivision in local and regional effects on metapopulation persistence is important in this context and a separate analysis of these effects as well.

The necessary analysis work in this study is based on the stochastic, spatially realistic metapopulation model presented in Chapter 2. This model consists of a generic main model and spatial submodels for integrating the landscape structure and the species' ecology. In the following, we (a) give a rough overview over central assumptions underlying the model and the current analysis, (b) specify the spatial submodels used, and (c) give a definition of and provide a measure for long-term metapopulation used in this study.

4.1.1 The main model and its central assumptions

We consider *finite* metapopulations of N patches, take the *stochasticity* in the sequence of extinction and colonization events in to account, but *ignore Allee and rescue* effects. In this case, stochastic Levins-type models such as the model in Chapter 2 are applicable.

The model assumes that the dynamics of the metapopulation are the result of *local extinction*, *correlated extinction*, and *recolonization* of the individual patches. Local extinction is assumed to occur with a probability per time ν_i, correlated extinction with $\rho_{ij}\sqrt{\nu_i}\sqrt{\nu_j}$, and recolonization with $\sum_{j(x_j=1)} c_{ji}$, where the sum is taken over all patches j currently occupied. The ν_is are the local extinction rates, the ρ_{ij}s the degrees of correlation, and the c_{ij}s the colonization rates. These parameters are the main model parameters.

We focus on metapopulations which successfully approached *quasi-stationarity* before extinction, i.e. show typical fluctuations in the occupancy and go extinct with a constant rate. In this case, the mean lifetime T_m is known to summarize all the effects of the local and regional dynamics which are relevant for metapopulation persistence. Therefore, T_m is an adequate measure for metapopulation persistence in this case (remember Chapter 2).

4.1.2 The submodels to include landscape structure and species ecology

In Chapter 2, various submodels are presented which relate the main model parameters to landscape structure and species' ecology. In the present study, it is particularly important that local and regional effects on metapopulation persistence can be separately analyzed.

4.1.2.1 The submodel for the colonization rate

We use the following submodel for the colonization rate from patch i to patch j:

$$c_{ij} = E_i \cdot a_{ij}. \tag{4.1}$$

where E_i denotes the number of emigrants local population i emits per time on average and a_{ij} the arrival probability, i.e. the probability that a disperser from patch i successfully reaches patch j. To integrate species' dispersal and the spatial structure of the habitat network, we use the simplest submodel for the arrival probability a_{ij}:

$$a_{ij} = \frac{1}{N-1} \cdot \mathrm{DISP}(d_{ij}), \tag{4.2}$$

where DISP is a certain dispersal function and d_{ij} is the distance between patches i and j. The shape of the dispersal function, DISP, depends on the species' movement characteristics (movement pattern, dispersal mortality), which may differ between habitat types (Kareiva and Shigesada 1983; Tischendorf and Wissel 1997; Heinz et al. 2005). The critical distance d_a above which $\mathrm{DISP}(d) \approx 0$ is no other than the specific *dispersal range* defined to be the maximum distance which can be covered by an individual disperser.

Submodel (4.2) implies that the arrival probability is *symmetric* ($a_{ij} = a_{ji}$) between two patches i and j. It is completely determined by the distance d_{ij} between the two patches. This indicates that we implicitly assumed the simplest dispersal strategy with competition between the patches for emigrants, namely corridor-oriented dispersal, and a complete pattern of connectedness. This was done to avoid an overloading of the study with too many interactions between the patches.

4.1.2.2 The submodel for the degree of correlation

The degree of correlation ρ_{ij} of the extinction processes in two patches i and j may decrease with the distance d_{ij} between them. We use the following submodel to cover this effect:

$$\rho_{ij} = \mathrm{CORR}(d_{ij}), \tag{4.3}$$

where CORR is a certain correlation function. Its shape depends on both the varying environmental factors and their species-specific effect on the local population dynamics. The critical distance d_ρ above which $\mathrm{CORR}(d) \approx 0$ is the species-specific *correlation length* defined to be the maximum distance over which the correlation acts.

To summarize, the presented submodels (4.1; 4.2; 4.3) relate the metapopulation dynamics to both the habitat network (local attributes (ν_i, E_i), patch configuration (d_{ij})) and the species' ecology ((DISP, d_a), (CORR, d_ρ)). They provide the basis for a separate investigation of local and regional effects on metapopulation persistence. While all the local effects are summarized in (ν_i, E_i), all the regional effects are summarized in (a_{ij}, ρ_{ij}).

4.1.3 The formula for the mean lifetime T_m^a for supplementary persistence analyses

All the analyses of metapopulation persistence in the present study are based on the values of the mean lifetime T_m numerically determined from the underlying model. Sometimes, however, it is useful to supplement the numerical work with analyses of the functional structure of the mean lifetime T_m. To meet the latter goal, we use of the approximation formula T_m^a deduced in Chapter 3. As we have shown, the mean lifetime T_m of a metapopulation in heterogeneous landscapes can be approximated by the following formula:

$$T_m \;\approx\; T_m^a \;:=\; \frac{1}{\nu_{agg}} \cdot e^{\frac{N}{(c_{tot}/\nu)_{agg}}} \cdot a(N, \rho_{agg}) \cdot \left((\frac{c_{tot}}{\nu})_{agg} \right)^{b(N,\rho_{agg})} \tag{4.4}$$

with the functions for the pre-factor $a(N,\rho)$ and the power $b(N,\rho)$ given in Table 3.III and the effective parameters ν_{agg}, ρ_{agg}, and $(\frac{c_{tot}}{\nu})_{agg}$ given by

$$\nu_{agg} = \prod_{i=1}^{N} {\nu_i}^{\frac{1}{N}}; \tag{4.5}$$

$$\rho_{agg} = \frac{1}{N(N-1)} \cdot \sum_{i=1}^{N} \sum_{j(\neq i)} \rho_{ij}; \tag{4.6}$$

$$(\frac{c_{tot}}{\nu})_{agg} = \prod_{i=1}^{N} \max\left(\sqrt{2}, \underbrace{\frac{\sqrt{\left[\frac{1}{2}\left\{(\sum_{j(\neq i)} c_{ij})^{-2} + (\sum_{j(\neq i)} c_{ji})^{-2}\right\}\right]^{-1}}}{\nu_i}}_{=:z_i}\right)^{\frac{1}{N}}. \tag{4.7}$$

The most complex term is the formula for $(\frac{c_{tot}}{\nu})_{agg}$. This term is determined by the local extinction rate ν_i and two sums of the colonization rates, $\sum_{j(\neq i)} c_{ij}$ and $\sum_{j(\neq i)} c_{ji}$, of the individual patches. The first sum equals the total number of colonizations patch i can induce per time when occupied. The second sum equals the total probability that patch i becomes recolonized after an extinction and can be interpreted as a measure of "actually being in the play". Therefore, the term under the square root can be interpreted as the *effective* colonization rate of patch i. However, as the max-function in the formula indicates, all these factors only contribute to $(\frac{c_{tot}}{\nu})_{agg}$ and so to T_m if $z_i > \sqrt{2}$, i.e. if patch i is at least so strong that its effective colonization rate exceeds its local extinction rate ν_i by a factor of $\sqrt{2}$. Otherwise, this patch does not significantly contribute to T_m. In this study, we assume that all the patches are strong enough, i.e. $z_i > \sqrt{2}$. Relation (4.4) has serious implications for the analysis of long-term metapopulation persistence.

4.1.3.1 Definition and measure of long-term metapopulation persistence

Relation (4.4) indicates that the mean lifetime T_m of the metapopulation is proportional to the effective mean lifetime $T_{agg} = \frac{1}{\nu_{agg}}$ of its local populations. This fact allows T_{agg} to be chosen as a time scale for the metapopulation dynamics. The relative ratio T_m/T_{agg} quantifies the survival advantage of the metapopulation over its local populations. *Long-term metapopulation persistence* is said to be obtained if T_m/T_{agg} is significantly large.

4.1.3.2 Measures for the local and regional effects on persistence

Relation (4.4) indicates that all the effects which are relevant for the survival advantage T_m/T_{agg} of a metapopulation are summarized in N, ρ_{agg}, and $(\frac{c_{tot}}{\nu})_{agg}$. With our settings for the colonization rates $c_{ij} = \frac{E_i}{N-1} \cdot a_{ij}$ (see (4.1)), we see that $(\frac{c_{tot}}{\nu})_{agg} = \frac{E_{agg}}{\nu_{agg}} \cdot a_{agg}$ with the effective number of emigrants E_{agg} and the effective arrival probability a_{agg} given by

$$a_{agg} \;=\; \prod_{i=1}^{N} (\sum_{j(\neq i)} a_{ij})^{\frac{1}{N}} \qquad \text{and} \tag{4.8}$$

$$E_{agg} \;=\; \prod_{i=1}^{N} \sqrt{\frac{{E_i}^2 \cdot (\sum_{j(\neq i)} E_j \cdot w_{ji})^2}{\frac{1}{2}\left({E_i}^2 + (\sum_{j(\neq i)} E_j \cdot w_{ji})^2\right)}}^{\frac{1}{N}} \;. \tag{4.9}$$

The weights w_{ji} are given by $w_{ji} = \frac{a_{ji}}{\sum_{k(\neq i)} a_{ki}}$ (note that $a_{ij} = a_{ji}$ in our case).

In the present study, we assume that the variance in the local attributes (ν_i, E_i) is at most moderate, in order to avoid an overloading with too many details (for a detailed analysis of the role of the local factors, see Chapter 5). In the result, the formula for E_{gg} further simplifies to a geometric mean, i.e. $E_{agg} \approx \prod_{i=1}^{N} {E_i}^{\frac{1}{N}}$, as the calculation in the Appendix shows. This quantity is independent of the a_{ij}s and so the spatial configuration.

All these arguments give rise to the following conclusions: Firstly, all the local effects which are relevant for the survival advantage T_m/T_{agg} of a metapopulation are summarized in the ratio $\frac{E_{agg}}{\nu_{agg}}$. This ratio gives the (effective) total number of emigrants a local population emits during its (effective) lifespan $\frac{1}{\nu_{agg}}$ and can be interpreted as effective colonization potential of the local populations. Secondly, all the relevant regional effects are summarized in the effective degree of correlation ρ_{agg} and the effective arrival a_{agg}. These three measures $(\frac{E_{agg}}{\nu_{agg}}, \rho_{agg}, a_{agg})$ can be used to distinguish between local and regional key factors of long-term metapopulation persistence in heterogeneous landscapes.

4.2 Results

The present study aims at answering the following questions: “What minimum conditions have to be met by the species’ ecology and the spatial structure of the habitat network (esp. scale and type of the patch configuration) before a metapopulation can benefit from landscape changes and persist over a long term?", "Is it possible to condense the scientific results of this study in verbal rules of thumb for conservational landscape management? Do these rules correspond with the existing rules of thumb?"

The individuals' specific perception of the landscape determines the effect on metapopulation persistence which can be obtained at all by changing the landscape structure. Therefore, rules of thumb for landscape management can only be deduced when both the concrete species and the concrete landscape are taken into account. However, because of the multitude of species-ecological and landscape-structural factors to be considered it is almost impossible to directly determine the real key factors of metapopulation persistence.

This dilemma can be avoided by using a *hierarchical* approach for the model analysis. In a *first* step, all metapopulation factors are assumed to be spatially homogeneous. This allows their relative importance for metapopulation persistence to be simply analyzed. In a *second* step, all factors which have been found to be limiting for metapopulation persistence are specified in a spatially heterogeneous way. In particular, both the landscape structure and the species' ecology are taken into account in this phase. Based on this, landscape-structural and species-ecological conditions can be revealed which have to be met before long-term metapopulation persistence can genuinely be attained.

4.2.1 The spatially homogeneous reference case

We start with assuming spatial *homogeneity*, i.e. all patches are identical with equal parameters ($\nu_i = \nu$, $E_i = E$, $a_{ij} = a$, $\rho_{ij} = \rho$). This allows the topic of long-term metapopulation persistence to be tackled from a *simple* side. Moreover, the corresponding results can be used as a *reference* for the spatially heterogeneous case considered later (Sec. 4.2.2).

Figure 4.1 shows the survival advantage T_m/T_{agg} of a homogeneous metapopulation with $N = 5$ patches in relation to degree of correlation ρ and arrival probability a for different levels of the colonization potential $\frac{E}{\nu}$ of the local populations. Figure 4.1A indicates that, whenever the degree of correlation ρ exceeds the critical value of 0.2, the metapopulation only has a low survival advantage T_m^h/T_l, even if the colonization potential of the local populations $\frac{E}{\nu}$ is high and every emigrant arrives ($a = 1$). Figure 4.1B, on the

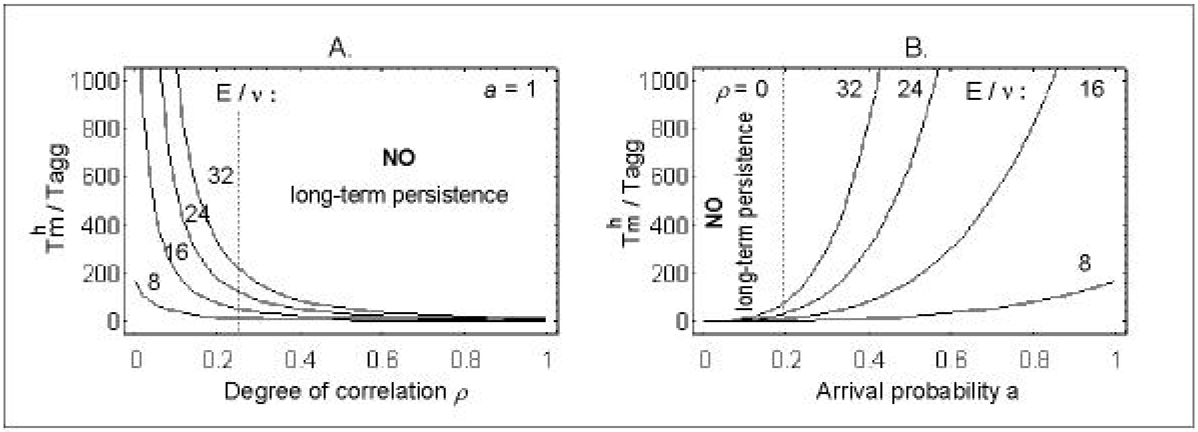

FIGURE 4.1: The survival advantage T_m^h/T_{agg} of a homogeneous metapopulation with 5 patches and parameters (ν, E, a, ρ). (a) T_m^h/T_{agg} versus the degree of correlation ρ for $a = 1$ and different levels of the colonization potential E/ν of the local populations. (b) T_m^h/T_{agg} versus the arrival probability a for $\rho = 0$ and different levels of E/ν. The broken lines in (a) and (b) mark the regions where is no chance of long-term persistence.

other hand, reveals that, as long as the arrival probability a is below the critical value of 0.2, really high values of T_m^h/T_l cannot be obtained, even if the local populations have a relatively high colonization potential $\frac{E}{\nu}$ and the correlation completely disappears ($\rho = 0$). Last but not least, both figures show that the metapopulation has no chance of persisting in the long term as long as the colonization potential $\frac{E}{\nu}$ of the local populations is below a certain minimum, regardless of the values of both ρ and a (see Figs. 4.1A-B).

To summarize, a homogeneous metapopulation can only persist in the long term if the following three conditions are met: (1) a minimum colonization potential $\frac{E}{\nu}$ of the local populations, (2) a low degree of correlation ρ, and (3) a minimum arrival probability a.

4.2.2 The spatially heterogeneous case

Now we pass on to the main part of this study – the determination of minimum conditions to be met by the species and the habitat network to allow long-term metapopulation persistence. In order to meet this goal, we abandon the assumption of having identical model parameters. We allow individuality in the local attributes $\{E_i, \nu_i\}$ and relate both the arrival probability a_{ij} and the degree of correlation ρ_{ij} to the patch configuration and the species' ecology by using the submodels () specified in Section 4.1.2.

In a first model experiment, we determine some species-ecological conditions (DISP, CORR) under which metapopulation persistence is actually sensitive to a change in the landscape structure. This results in a characterization of the species which can perceptibly benefit from metapopulation management. In a second model experiment, we analyze the role of the spatial structure of the habitat networks for metapopulation persistence and give a characterization of favorable patch configurations.

4.2.2.1 Conditions governing the species' ecology

To analyze the role of the species' ecology, we assume a certain correlation type (CORR, d_ρ) and consider two dispersal types (DISP, d_a), namely short-distance dispersal ($d_a < d_\rho$) and long-distance dispersal ($d_a > d_\rho$). We assume patch-specific attributes of the local populations (ν_i, E_i). In order to avoid an overloading of the study with too many spatial details, we start with "Equi", a hypothetical equidistant configuration ($d_{ij} = d$).

We analyze the extent to which species' dispersal influences the chance of obtaining long-term metapopulation persistence through a change in the local ($\frac{E_{agg}}{\nu_{agg}}$) or the spatial ($d$) settings. Figures 4.2A-B show the result for short-distance dispersal. In this case, the dispersal range d_a is below the correlation length d_ρ such that DISP$(d_c) \approx 0$ (see Fig. 4.2A).

TABLE 4.I

The sets of the specific subpopulation features $\{(\nu_i, E_i)\}$ for the metapopulations analyzed in Figs. 4.2C and 4.2D and in Figs. 4.3C-D respectively.

A		**B**		**C**		**D**		**E**		**F**	
ν_i	E_i	ν_i	E_i	ν_i	E_i	ν_i	E_i	ν_i	E_i	ν_i	E_i
0.2	6	0.3	6	0.2	10	0.3	10	0.2	2	0.2	2.4
0.4	12	0.8	12	0.4	5	0.8	5	0.4	8	0.4	4.8
0.6	20	0.7	20	0.6	7	0.7	7	0.6	18	0.6	16.2
0.8	24	0.6	24	0.8	25	0.6	25	0.8	32	0.8	9.6
1	40	0.85	40	1	15	0.85	15	1	50	1	12

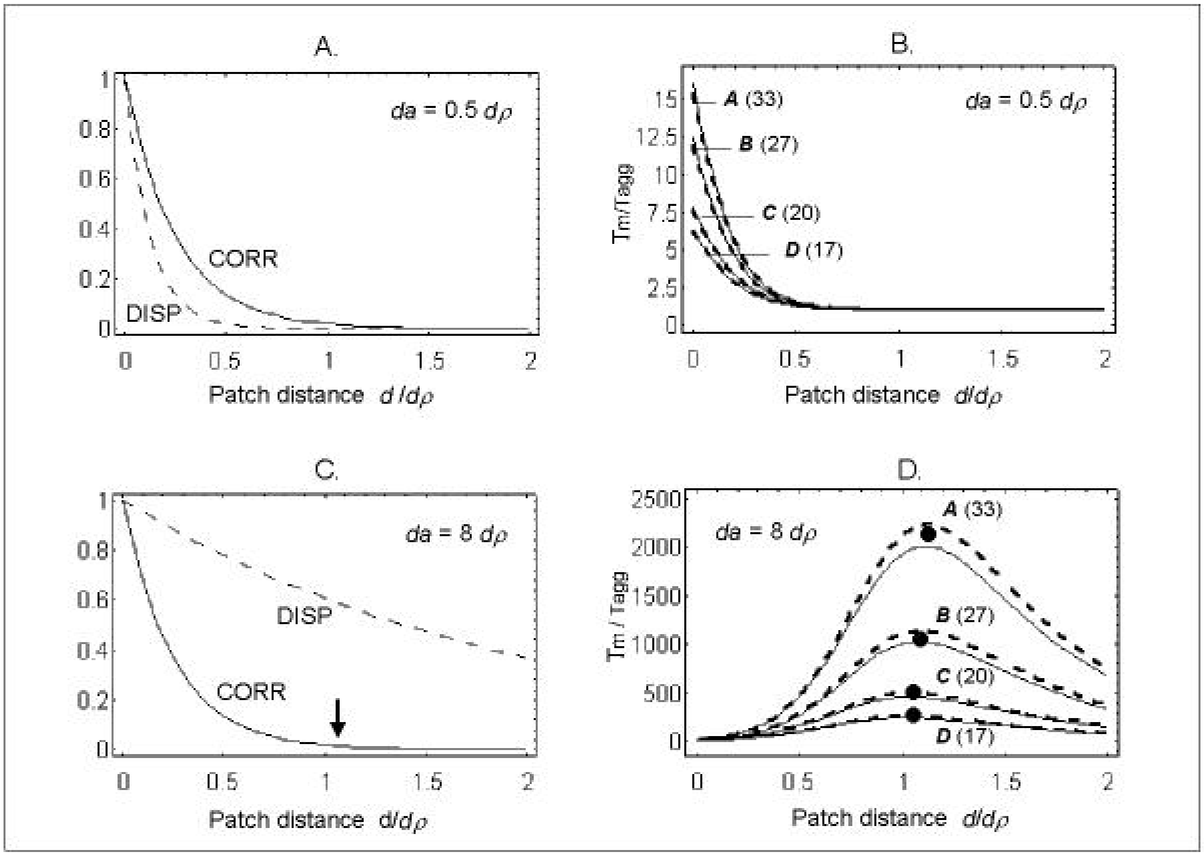

FIGURE 4.2: The distance dependence of degree of correlation $\rho(d) = \mathrm{CORR}(d) = e^{-4d/d_\rho}$ and arrival probability $a(d) = \mathrm{DISP}(d) = e^{-4d/d_a}$ for short-distance dispersal ($d_a = 0.5 d_\rho$; (A)) and long-distance dispersal ($d_a = 8 d_\rho$; (C)). (B) and (D): Mean lifetime T_m/T_{agg} for a metapopulation with 5 equidistant patches ($d_{ij} = d$) versus patch distance d (scaled by d_ρ) for the local attributes $\{E_i, \nu_i\}$ given in **A-D** of Tab. 4.I. The broken lines correspond to a homogeneous metapopulation with identical parameters (ν_{agg}, E_{agg}) defined in (4.8;4.9). The values in the parentheses denote the resulting effective colonization potential of the local populations $\frac{E_{agg}}{\nu_{agg}}$.

Figure 4.2B indicates that the survival advantage T_m/T_{agg} of the metapopulation goes up when the patch distance d decreases. Nevertheless, the metapopulation has no chance of persisting over a long term, even if its patches are close to each other and the effective colonization potential $\frac{E_{agg}}{\nu_{agg}}$ of its local populations increases. A totally different picture emerges in the case of long-distance dispersal where the dispersal range d_a exceeds the correlation length d_ρ. Here, the individuals have a real chance of escaping the range of correlation ($\mathrm{DISP}(d_c) > 0$; see Fig. 4.2C). In this case, there is a critical patch distance

$d_o \approx d_\rho$ that is optimum for survival, namely where the correlation ρ becomes very low (compare the bullets in Fig. 4.2D with the arrow in Fig. 4.2C). Markedly below or above the optimum d_o, the metapopulation only has a low survival advantage T_m/T_{agg}, regardless of the effective colonization potential $\frac{E_{agg}}{\nu_{agg}}$ of its local populations. However, as long as $\frac{E_{agg}}{\nu_{agg}}$ is below a certain minimum, the metapopulation has no chance either of persisting over a long term, even if patch distance d is optimum.

To summarize, only if the species under discussion exhibits long-distance dispersal ($d_a > d_\rho$), there is a real chance of inducing any noticeable effect on metapopulation persistence through local and/or spatial landscape management. Long-term metapopulation persistence, however, can only be obtained if landscape management is able to ensure both (a) an effective colonization potential $\frac{E_{agg}}{\nu_{agg}}$ of the local populations that exceeds a certain minimum and (b) a patch distance d that is near the optimum distance $d_o \approx d_\rho$. Both conditions, the long-distance dispersal and the optimum patch distance, result from the necessity to implement both a low degree of correlation ρ and a minimum arrival probability a, i.e. the persistence conditions found in the homogeneous case.

4.2.2.2 Conditions governing the patch configuration

In the following, we consider species which exhibit *long-distance dispersal*. Only these species have been found to perceptibly benefit from landscape management. We focus on the analysis of the effect of the patch configuration (a detailed analysis of the effect of the local settings is carried out in the next chapter of this thesis). After revealing how the patch configuration influences metapopulation persistence at all, we finalize with a characterization of those configurations which are favorable for long-term persistence.

We consider metapopulations with patch-specific local populations. Additionally, we abandon the assumption of an equidistant configuration. To cover a large range of reasonable patch configurations, we analyze its extreme examples, the one-dimensional “Chain” (Fig. 4.3Aa) and the two-dimensional “Array” (Fig. 4.3B). To attain comparability, both configurations are scaled by the distance d between central patch 3 and its direct neighbors (2 and 4). Now the basis is given for analyzing the way metapopulation persistence is influenced by the *scale* (d) and *type* (relative form) of the patch configuration.

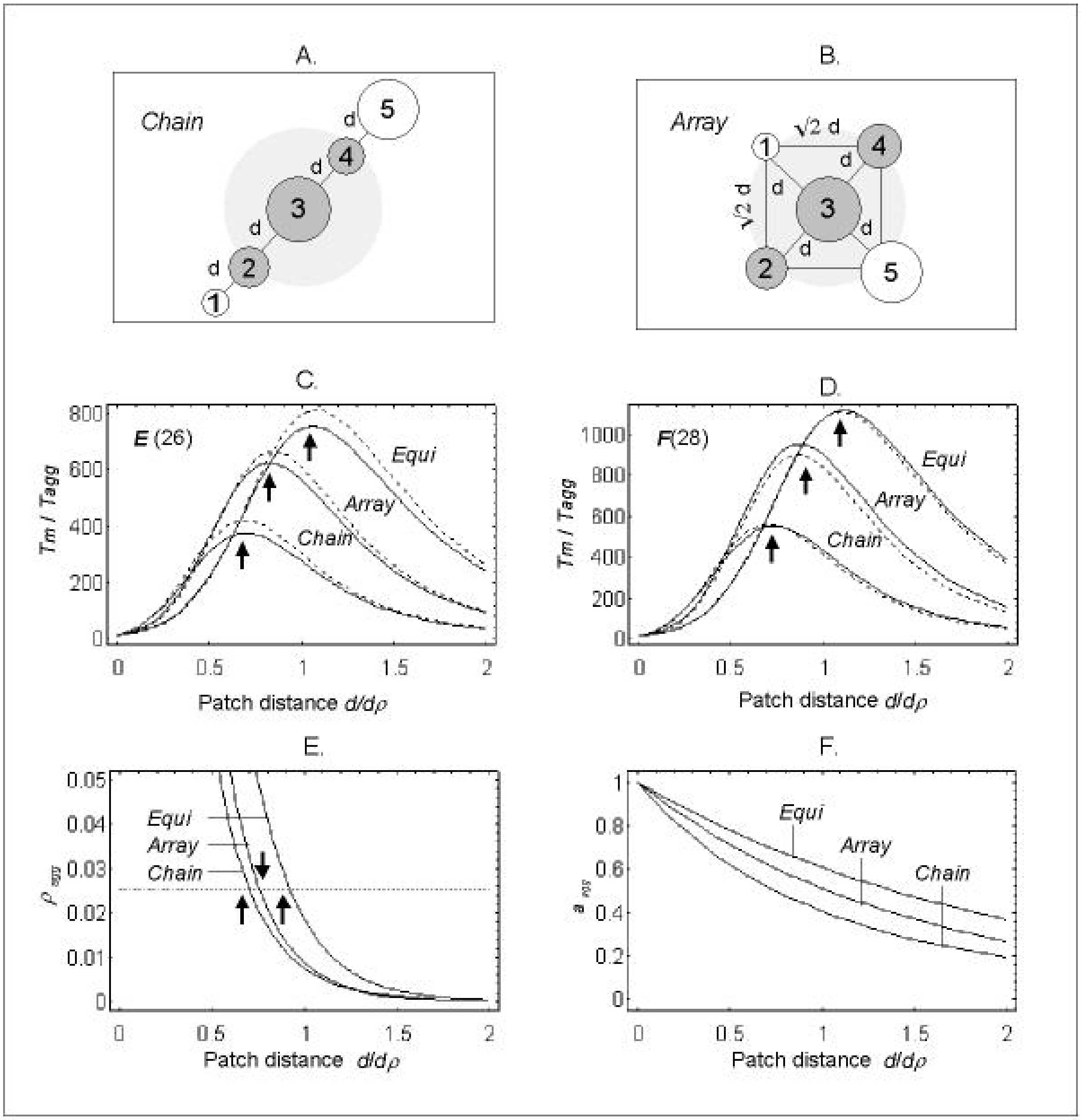

FIGURE 4.3: Two configurations of 5 patches are considered: the one-dimensional "Chain" (A) and the two-dimensional "Array" (B). Both configurations are scaled by the distance d between the central patch and its nearest neighbors. (C) and (D): The survival advantage T_m/T_{agg} of a metapopulation living in an "Array", a "Chain" or an equidistant configuration "Equi" versus the patch distance d for the local attributes given by **E** and **F** of Tab. 4.I. In both cases, long-distance dispersal with settings as in Fig. 4.2D is assumed. The broken lines correspond to a homogeneous metapopulation with identical parameters $(\nu_{agg}, \frac{E_{agg}}{\nu_{agg}}, a_{agg}, \rho_{agg})$ defined in (4.8; 4.9). The values in parentheses are the resulting values of $\frac{E_{agg}}{\nu_{agg}}$. The effective ρ_{agg} (E) and the effective a_{agg} (F) versus the patch distance d for the configuration types under discussion.

Figures 4.3C-D show the survival advantage T_m/T_{agg} of the metapopulation in relation to the patch distance d for the patch configurations under consideration and various sets of local attributes. Evidently, for every configuration type, there is an optimum patch distance d_o (Figs. 4.3C-D), namely where the corresponding effective degree of correlation ρ_{agg} becomes very low (cf. the arrows in Fig. 4.3E). All these optimum distances d_o roughly coincide with the correlation length d_ρ. This corresponds with the results in the equidistant case and corroborates that both the existence and magnitude of the optimum distance $d_o \approx d_\rho$ are common effects and not artifacts of a concrete configuration.

Our results (Figs. 4.3C-D) also indicate that deciding in general which configuration type is most favorable for metapopulation persistence is impossible. As long as the patch distance d is above the optimum $d_o \approx d_\rho$, the configuration type is decisive for the survival advantage T_m/T_{agg}. The "Array" has a clear advantage over the "Chain". Since all configurations are almost free of correlation (see Fig. 4.3E), the effective arrival probability a_{agg} becomes limiting. The "Array" produces the higher a_{agg} (Fig. 4.3F) because its peripheral patches (1 and 5) are closer to the central patch than those of the "Chain". Moreover, the comparison with the equidistant configuration ("Equi") shows that there is a hierarchy of importance among the configuration types ("Equi" ▷ "Array" ▷ "Chain"). This means that the more balanced the distances between the patches are, the longer can the metapopulation persist. A totally different picture emerges if the patch distance d is markedly below the optimum $d_o \approx d_\rho$. In this case, the hierarchy of importance among the configuration types completely changes ("Chain" ▷ "Array" ▷ "Equi"). This effect can be traced to the effective degree of correlation ρ_{agg} that is now high enough to become dominating. The top position of the "Chain", for instance, is due to its peripheral patches (1 and 5) which are more distant to the central patch than those of the "Array" and the equidistant configuration "Equi". The "Chain" produces the lowest ρ_{agg} (see Fig. 4.3E) and, therefore, the highest chance of survival. But Figures 4.3C-D also show that the magnitude of T_m/T_{agg} is rather low, regardless of the configuration type.

To summarize, the answer to the question about which configuration type is more favorable for metapopulation persistence closely depends on the patch distance d and its relationship to the optimum $d_o \approx d_\rho$. Long-term metapopulation persistence can only be obtained if $d > d_\rho$, i.e. if no patch is inside the range of correlation of another one. Hence, we get as a *landscape-structural equivalent* to the persistence conditions in the homogeneous reference case: "First optimize the patch distance, then optimize the configuration type." This demonstrates the importance of a correct patch choice in the run-up to configuration design. For all these results (optimum patch distance, optimum configuration type, and persistence conditions to be met by spatial configurations), the specific local population features (E_i, ν_i) are of no bearing (cf. Figs. 4.3C and 4.3D).

4.3 Discussion

The results of this study indicate that certain minimum conditions on both the species' ecology (CORR, DISP) and the spatial structure of the habitat network (e.g. local attributes, scale and type of patch configurations) must be met before a metapopulation can persist over a long term. The species-ecological conditions indicate which species can benefit from landscape changes at all. The landscape-structural conditions determine the scope a concrete measure ought to target to support species' survival most efficiently. The attained model results have serious implications for both metapopulation theory and conservation management. They provide new insights into the requirements of landscape analyses from the perspective of metapopulation persistence, allow a qualification/modification of existing rules of thumb for landscape management, disclose some principle limitations of supporting species survival by conservational landscape management, and give rise to some consequences for empirical and theoretical research.

4.3.1 Implications for the landscape analysis

4.3.1.1 Correlation length as spatial scale for metapopulations

The results presented merely depend on the relationship between the dispersal range d_a (or patch distance d) and the correlation length d_ρ. Thus d_ρ defines a *spatial scale* for any metapopulation dynamics and provides a yardstick for estimating the survival advantage from both the species-ecological (d_a) and the landscape-structural (d_{ij}) point of view. Whenever d_ρ is neglected, a totally distorted picture of metapopulation persistence occurs.

4.3.1.2 A hierarchy of importance among the different spatial factors

One important result of this study is the finding that the different factors ((CORR, d_ρ), (DISP, d_a), local attributes, scale/type of patch configuration) are *not* of the same value for metapopulation persistence: As long as the species' dispersal fails the condition required ($d_a > d_\rho$), there is no chance of obtaining long-term metapopulation persistence through a change in the spatial structure of the habitat network. Furthermore, an appropriate configuration scale is needed ($d_o > d_\rho$) before the configuration type becomes limiting. This leads to the following hierarchy of importance among the spatial factors analyzed:

$$\text{dispersal range} \quad \triangleright \quad \text{configuration scale} \quad \triangleright \quad \text{configuration type.}$$

This hierarchy is valid as long as rescue effects do not play a perceptible role. In this case, all the local attributes and, hence, all the details of the local dynamics have been found to be of no bearing (Sec. 4.2.2). This fact has serious consequences for the management:

The hierarchy indicates that a change in a certain factor is useless as long as not all persistence conditions governing factors "higher" in the hierarchy are really met. In this case, the scope of management ought to be changed or a certain preparatory management ought to implement the conditions required. The knowledge of all these relationships increases the chance of investing scarce resources with higher effects on survival.

4.3.2 Rules of thumb for landscape management

The following rules of thumb for landscape management reflect the hierarchy of importance found. Some of them qualify the well-known rules for reserve network design by Wilson and Willis (1975; see also Figure 4.4) and indicate needs of their modification.

4.3.2.1 In the run-up to metapopulation management

As seen above, as long as the species' dispersal range d_a is lower than the correlation length d_ρ, the survival advantage T_m/T_{agg} of the metapopulation over its local populations is in principle low. In this situation, metapopulation management (choose, arrange and connect patches) is *not yet* the right approach to support the species in persisting over

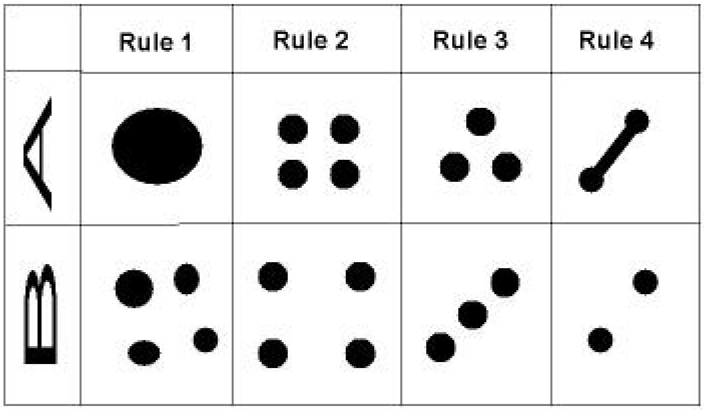

FIGURE 4.4: Some "island biogeographic" rules for reserve design (after Wilson and Willis 1975). In each case, the design in the A-row is seen as superior to the alternative in the B-row.

a long term. Alternative forms of management are needed. However, it is necessary to draw a distinction between a *natural* and a *man-made* discordance between d_a and d_ρ.

A natural discordance between d_a *and* d_ρ

There is a hypothesis (Hanski 1991) that species which are naturally adapted to a correlated environment have other life history strategies than "dispersal". In this case, the dispersal range d_a is below the correlation length d_ρ such that the species cannot in principle benefit from a metapopulation. There is no alternative to the long-term persistence of the local populations. Thus, local habitat management is needed which supports the individuals in handling environmental effects within the local populations themselves.

A man-made discordance between d_a *and* d_ρ

A totally different situation occurs if the discordance between the species' dispersal range d_a and the correlation length d_ρ is man-made. As the model results indicate, these negative effects cannot be offset by metapopulation management alone. Thus, in the run-up, preparatory management is needed which must be focused on restoring the accordance between d_a and d_ρ. As a rule of thumb we can formulate:

"Restore the accordance between d_a *and* d_ρ *first."*

Increase d_a *and/or diminish* d_ρ*.*

To illustrate this, two examples are given which show how changing *land use* can destroy and restore the accordance between the dispersal range d_a and the correlation length d_ρ:

During their study of a transhumant flock of sheep, Fischer *et al.* (1995) identified 27 animal species (grasshoppers and snails) spread by sheep. Experiments showed that grasshoppers can be dispersed over more than 100 m when sheep are grazing and over more than 500 m when sheep are roaming. Hence, shepherding (especially transhumance) is a key factor for long-distance dispersal and is crucial for species with a low radius of activity. However, the dispersal system of *tending grazing herbivores* has almost totally vanished (Poschlod *et al.* 1996). Therefore, it is important to retain low-intensity farming systems as vehicles for transport and key factors for long-term metapopulation persistence.

As Settele and Geißler (1988) show, the extensive decline of the Dusky Large Blue butterfly (*Maculinea nausithous*) can be related to a change in the mowing regime for meadows. *Maculinea nausithous* is highly specialized to its host plant *Sanguisorba officinalis*. Thus the species is very sensitive to mowing. Cutting before September exterminates the host plants and all inhabited stages of the butterflies (eggs, larvae) such that local populations inside the whole range of mowing will go extinct simultaneously. In this case, *small-scale mowing* (different parts in different years) which leads to the de-synchronization of the extinction processes and, hence, the shortening of the critical correlation length d_ρ, becomes a key factor of metapopulation persistence.

4.3.2.2 Rules for choosing the right patches for linking

Whenever the species' dispersal range d_a exceeds the correlation length d_ρ, there is a potential chance of obtaining long-term metapopulation persistence. The optimum patch distance $d_o \approx d_\rho$ found gives rise to a rule for choosing the right patches for linking:

"As near as possible, but as far away as necessary."
Only integrate patches which are outside the range of correlation
into the metapopulation network.

This contrasts with the well-known rule for reserve network design (Wilson and Willis 1975; Wilcove *et al.* 1986; cf. Rule 2 in Fig. 4.4) that *clumping*, i.e. the integration of those patches which are *"as near as possible"*, produces the maximum effect on survival.

Our rule results from the *trade-off* (see also Hanski 1991) between an increasing arrival probability (a_{ij}) and an increasing spatial correlation of extinction (ρ_{ij}). This effect, however, only appears if the distance-dependence of the correlation is taken into account.

Whenever choosing patches for linking outside the range of correlation is impossible, management ought to be concentrated on supporting the local populations. But every planner ought to have in mind that, in this case, "*chains are more favourable than arrays*" as a rule. This contrasts with another well-known rule for reserve design (Wilson and Willis 1975; Rule 3 in Fig. 4.4), namely that "*arrays are always better than chains*". As before, our rule results from the effects of the distance-dependent correlation.

4.3.2.3 Rules for designing optimum patch configurations

Whenever the patch distance d is above the optimum $d_o \approx d_\rho$ such that no patch is inside the range of correlation of another, the configuration type becomes important for metapopulation persistence. As a rule for designing optimum configurations we obtain:

"As homogeneous as possible."
Arrays are more favourable than linear chains.

Exactly ensuring optimum circumstances in all situations is doubtless impossible. However, knowing the optimum enables the planner to decide out of a variety of possible management alternatives which variant is best. This increases the chance of investing management effort with maximum effect on species survival.

4.3.3 Limitations of supporting species survival by management

4.3.3.1 There is no general recipe for species conservation management

It is *impossible* to deduce general rules of thumb for management which are valid for all species and all landscapes. The life history of the species determines what kind of management is suitable for survival support at all. Thus only for *classes* of species with a common ecological *profile* (Grimm *et al.* 1996; see also the resilience profile in Weaver *et al.* 1996) can common rules of thumb for conservation management be deduced.

4.3.3.2 No management measure is efficient for species survival per se

Every management measure requires some species-ecological and landscape-structural set-up before it can become efficient at all. This fact has serious consequences: (1) To deal with the landscape-structural conditions found, certain preparatory measures in the run-up to the planned measure are needed. This means that there is a clear order concerning the measures to be applied. (2) Regardless of the preparation, only those species which fulfill the species-ecological conditions encountered have a real chance of benefiting from the planned measure at all. Knowledge of both the *preparatory management* needed and the *benefiting species* allows the effects of the planned measure to be estimated beforehand.

4.3.4 Consequences for empirical and theoretical research

The model results indicate the ecological factors which are to be primarily targeted in the realm of empirical and theoretical research: the species' dispersal behavior (summarized in DISP, d_a) and the correlation of the extinction processes (summarized in CORR, d_ρ). If detailed submodels are used to determine the concrete forms of the functions DISP and CORR then the resulting relationships are much closer to reality than ad hoc assumptions such as the often used exponential decrease (Harrison *et al.* 1988; Gyllenberg and Silvestrov 1994; Hanski 1994; Frank and Wissel 1998, 2002; Grimm *et al.* 1996).

4.3.4.1 Determination of the species' dispersal range

Direct determinations of the species' dispersal range d_a are very difficult (Doak and Mills 1994). Moreover, d_a does not only depend on the (habitat-specific) movement pattern (Marsh and Jones 1988; Kareiva and Shigesada 1993) or the dispersal mortalities, but also on the spatial structure of the landscape used. Hence, individual-based simulation models are needed to integrate movement behavior and landscape structure (Tischendorf and Wissel 1997; Wiegand et al. 1999; Tischendorf and Fahrig xxx; Schadt et al. xxx). With the help of such models, the species' dispersal range d_a or even the entire dispersal function DISP can be determined and analyzed (e.g. Moilanen and Hanski (xxx); Ovaskainen 2004; Heinz et al. 2005; Pe'er et al. 2005).

4.3.4.2 Studies on correlation length and de-synchronizing mechanisms

Whenever the correlation length d_ρ ought to be reduced, we need to know some mechanisms which support the desychronization of the local population dynamics. The following examples demonstrate how such a desynchronization can be obtained through *habitat diversity*. (1) Studies of the Bay Checkerspot butterfly *Euphydryas editha bayensis* show (Harrison *et al.* 1988) that habitats of different slopes have different microclimatic conditions implying different resource dynamics and so desynchronized local extinction processes. (2) For the Grey Bush cricket *Platycleis albopunctata* it has been found (Gottschalk 1996) that habitats of different successional stages lead to different microclimatic conditions, different reproduction rates and hence to desynchronized local extinction processes. In both cases local factors are able to counteract regional impacts.

4.3.4.3 Some prospects for further research

In the present study, we used a simple distance-dependent submodel for the arrival probability $a_{ij} = \frac{1}{N-1} \cdot \mathrm{DISP}(d_{ij})$. This means that we implicitly assumed a particular dispersal strategy (corridor-oriented dispersal in the special case of a complete pattern of connectedness (cf. submodel (2.15) in Section 2.2.3.2)). The species' dispersal strategy, however, has been found to be crucial for the effect of the patch configuration on metapopulation persistence (see Heinz et al. (submitted)). Therefore, it is worth to repeat the present study for other dispersal strategies. It can be expected that the results concerning whether an "Array" or a "Chain" is better for metapopulation persistence alter. However, also in this case, the explanation for the ranking order among the patch configurations is expected to be the same: in the case with correlation, the configuration with the lower ρ_{agg}-value is better and, in the uncorrelated case, the configuration with the higher a_{agg}-value.

4.4 Appendix

In the following, we demonstrate that the effective number of patches E_{agg} given by relation (4.9) simplifies to a geometric mean $\prod_{i=1}^{N} E_i{}^{\frac{1}{N}}$ in the case that the variance in the numbers of emigrants E_i is at most moderate. Evidently,

$$\begin{aligned} E_{agg} &= \prod_{i=1}^{N} \sqrt{\frac{{E_i}^2 \cdot (\sum_{j(\neq i)} E_j \cdot w_{ji})^2}{\frac{1}{2}\left({E_i}^2 + (\sum_{j(\neq i)} E_j \cdot w_{ji})^2\right)}}^{\frac{1}{N}} = \underbrace{\prod_{i=1}^{N} \sqrt{\frac{1}{\frac{1}{2}\left((\frac{E_i}{\sum_{j(\neq i)} E_j \cdot w_{ji}})^2 + 1\right)}}^{\frac{1}{N}}}_{\in\ 2/(\frac{E_{max}}{E_{min}}+1),\ 2/(\frac{E_{min}}{E_{max}}+1)} \cdot \prod_{i=1}^{N} {E_i}^{\frac{1}{N}} \\ &\approx \prod_{i=1}^{N} {E_i}^{\frac{1}{N}}, \qquad (4.10) \end{aligned}$$

where w_{ji} are weights given by $w_{ji} = \frac{a_{ji}}{\sum_{k(\neq i)} a_{ki}}$ (note that $a_{ij} = a_{ji}$ in our case). The underlined pre-factor is ≈ 1 in the case of moderate variation in the E_is ($\frac{E_{max}}{E_{min}}$ not too large). Hence, E_{agg} nearly coincides with a geometric mean of the E_is.

4.5 References

Baars, M.A. and van Dijk, T.H. (1984). Population dynamics of two carabid beetles at a Dutch heathland. I. Subpopulation fluctuations in relation to weather and dispersal. J. Animal Ecology 53: 375–388

den Boer, P.J. 1981. On the survival of populations in a heterogeneous and variable environment. Oecologia (Berlin) 50: 39–53

Doak, D.F. and Mills, L.S. 1994. A useful role for theory in conservation. - Ecology. 75: 615-626.

Drechsler, M. and Wissel, C. 1997. Separability of local and regional dynamics in metapopulations. Theor. Popul. Biol. (in press)

Errington, P.L. 1946. Predation and vertebrate populations. Q. Rev. Biol. 41: 315–336

Fischer, S., Poschlod, P. and Beinlich, B. (1996). Experimental studies on the dispersal of plants and animals by sheep in calcareous grasslands. Journal of Applied Ecology (in press).

Gilpin, M. 1990. Extinction of finite metapopulations in correlated environments. *In* Living in a Patchy Environment. pp. 177–186. Edited by B. Shorocks. Oxford University Press, Oxford

Goodman, D. 1987. The demography of chance extinction. *In* Viable Populations for Conservation. pp. 11–34. Edited by M.E. Soulè. Cambridge University Press, Cambridge

Gottschalk, E. 1996. Population vulnerability of the Grey Bush cricket *Platycleis albopunctata* (Goeze, 1778) (Ensifera: Tettigoniidae). *In* Species Survival in Fragmented Landscapes. pp. 324–328. Edited by J. Settele, C.R. Margules, P. Poschlod and K. Henle. Kluwer Academic Publishers, Netherlands

Grimm, V., Frank, K., Jeltsch, F., Brandl, R., Uchmański, J. and Wissel, C. 1996. Pattern-oriented modelling in population ecology. Science of the Total Environment 183: 151–166

Gyllenberg, M. and Silvestrov, D.S. (1994). Quasi-stationary distributions of a stochastic metapopulation model. J. Math. Biol. 33: 35-70

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biol. J. Linnean Society 42: 17–38

Hanski, I. 1994. A practical model of metapopulation dynamics. J. Anim. Ecol. 63: 151–162

Harrison, S., Murphy, D.D. and Ehrlich, P.R. 1988. Distribution of the Bay checkerspot butterfly, *Euphydryas editha bayensis*. Evidence for a metapopulation model. Am. Nat. 132: 360–382

Harrison, S. and Quinn, J.F. 1989. Correlated environments and the persistence of metapopulations. Oikos 56: 1–6

Kalkhoven, J.T.R. 1995. Application of knowledge on fragmentation in planning. *In* Principles and tools for the study of landscape ecology – potentials and limitations. Proceedings of the Second CONNECT Workshop in Landscape Ecology 1993 (NERI Technical Report no. 131). pp. 98–100. Edited by F. Skov, J. Komdeur, G. Fry and J. Knudsen. National Environmental Research Institute

Kareiva, P. and Shigesada, N. 1983. Analyzing insect movement as a correlated random walk. Oecologia (Berlin) 56: 234–238

Lefkovitch, L.P. and Fahrig, L. 1985. Spatial characteristics of habitat patches and population survival. Ecol. Modelling 30: 297–308

Levin, S.A. (1992). The problem of pattern and scale in ecology. Ecology. 73: 1943–1967

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull. of Entomol. Society of America 15: 237–240

Nagylaki, T., Keenan, P.T. and Dupont, T.F. (1993). The influence of spatial inhomogeneities on neutral models of geographical variation, III. Migration across a geographical barrier. Theor. Pop. Biology. 43: 217–249

Nisbet, R.M. and Gurney, W.S.C. 1982. Modelling Fluctuating Populations. Wiley, New York

Moloney, K.A. 1993. Determining process through pattern: reality or fantasy. *In* Patch Dynamics (Lecture Notes in Biomathematics 96) pp. 61–69. Edited by S.A. Levin, T.M. Powell and J.H. Steele. Springer-Verlag, Berlin

Poschlod, P., Bakker, J., Bonn, S. and Fischer, S. (1996). Dispersal of plants in fragmented landscapes. *In* Species Survival in Fragmented Landscapes. pp. 123–127. Edited by J. Settele, C.R. Margules, P. Poschlod and K. Henle. Kluwer Academic Publishers, Netherlands

Quinn, J.F. and Hastings, A. 1987. Extinction in subdivided habitats. Conservation Biology 1: 198–208

Schippers, P., Verboom, J., Knapen, J.P. and van Apeldoorn, R.C. 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. Ecography 19: 97–106

Schumaker, N.H. 1996. Using landscape indices to predict habitat-connectivity. Ecology. 77: 1210–1225

Settele, S. and Geißler, S. 1988. Schutz des vom Aussterben bedrohten Blauschwarzen Moorbläulings durch Brachenerhalt, Grabenpflege und Biotopverbund im Filderraum. Natur und Landschaft 11: 467–470

Sisk, T.D. and Margules, C.R. 1993. Habitat edges and restoration: methods for quantifying edge effects and prediciting the results of restoration efforts. *In* Reconstruction of Fragmented Ecosystems (Nature Conservation 3). pp. 57–69. Edited by D.A. Saunders, R.J. Hobbs and P.R. Ehrlich. Sarrey Beatty & Sons

Stelter, C., Reich, M., Grimm, V. and Wissel, C. 1997. Modelling persistence in dynamic landscapes: lessons from a metapopulation of the grasshopper *Bryodema tuberculata*. J. Animal Ecology (in press)

Tischendorf, L. 1997. Modeling individual movements in heterogeneous landscapes: potentials of a new approach. Ecological Modelling (in press)

Tischendorf, L. and Wissel, C. 1997. Corridors as conduits for small animals: Attainable distances depending on movement pattern, boundary reaction and corridor width. Oikos (in press)

Verboom, J., Lankester, K. and Metz, J.A.J. 1991. Linking local and regional dynamics in stochastic metapopulation models. Biol. J. Linnean Society 42: 39–55

Verboom, J., Metz, J. and Meelis, E. 1993. Metapopulation models for impact assessment of fragmentation. *In* Landscape Ecology of a Stressed Environment. (IALE Studies in Landscape Ecology 1). pp. 172–191. Edited by C.C. Vos and P. Opdam. Chapman & Hall, London

Wilcove, D.S., McLennan, C.H. and Dobson, A.P. 1986. Habitat-fragmentation in the temperate zone. *In* Conservation Biology. pp. 237–256. Edited by M.E. Soulé. Sinauer, Sunderland

Wilson G.G. and Willis, E.O. 1975. Applied biogeography. *In* Ecology and Evolution of Communities. pp. 523–534. Edited by M.L. Cody and J.M. Diamond. Harvard University Press, Cambridge, MA

Weaver, J.L., Paquet, P.C. and Ruggiero, L.F. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. Conservation Biology 10: 964–976

Wissel, C., Stephan, Th., and Zaschke, S.-H. 1994. Modelling extinction of small populations. *In* Minimum viable populations. (Ecol. Studies 106). pp. 67–103. Edited by H. Remmert

Wolfram, S. 1992. *Mathematica* - A System for Doing Mathematics by Computer. Addison-Wesley Publishing Company (Germany). 993 pp.

Chapter 5

Optimum patch size distribution in metapopulations

This chapter is mainly based on the following publication:

Frank, K. 2004. Ecologically differentiated rules of thumb for habitat network design – lessons from a formula. *Biodiversity and Conservation* 13: 189–206

In Chapter 4, we were primarily interested in the relative importance of the *patch configuration*, $\{(x_i, y_i) : 1 \leq i \leq N\}$, for metapopulation persistence and the role of the species' ecology in this context. We searched for *minimum conditions* on configuration and species that have to be met to allow long-term persistence. We also revealed which configurations are optimum and condensed all the scientific results in verbal rules of thumb.

Now we shift the focus of attention to another spatial aspect of habitat networks: the *patch size distribution* $\{A_1, .., A_N\}$, that depends on both the total amount of habitat A_{tot} in the network and its distribution p_i over the individual patches, i.e. $A_i = p_i \cdot A_{tot}$. To understand the role of the patch size distribution for metapopulation persistence and to know the optimum is important for both ecological theory and landscape management. It provides further insight into the interplay between spatial structure and ecological processes that is of general interest in ecology. It also supports a better understanding of the relative importance of the individual patches for the persistence of the overall metapopulation. This is crucial for setting correct management priorities in the reserve network design. However, there are *two particular challenges* in this context. Firstly, the effect of the patch size distribution on metapopulation persistence can only be fully understood if its interplay with the other spatial aspects of the habitat network and the species' ecology is taken into account. Hence, a combination of optimization and systematic variation work is needed. Secondly, it is neither possible nor useful to perform a detailed optimization analysis for each new species or each new landscape. Hence, rules of thumb are needed which give at least a rough orientation about the optimum.

Optimum patch size distributions are addressed in various studies with various degrees of detail: There are specific case studies of optimum reserve selection or reserve network design where the problem of patch size is discussed (e.g. van Langevelde *et al.* 2000, 2002; Haight et al. 2001; Andelman and Willig 2002; Westphal *et al.* 2003). In most of these cases, however, special numerical optimization algorithms such as the simulated annealing algorithm (e.g. Metropolis *et al.* 1953; Kirkpatrick *et al.* 1983) are used to determine the optimum. To combine these algorithms with systematic variations of the underlying landscape structure and of the species' ecology is almost impossible. This would require tremendous simulation work. This indicates that alternative approaches are needed to attain a comprehensive mechanistic understanding of the optimum and to derive appropriate rules of thumb as required. There are also theoretical studies on the effect of the patch size distribution on metapopulation persistence (Anderson 1991; Doak *et al.* 1992; Hanski and Gyllenberg 1993; Hanski 1994; Frank and Wissel 2002; Hanski and Ovaskainen 2000; Ovaskainen and Hanski 2003; Frank 2004). These studies usually assume hypothetical species in hypothetical landscapes. Etienne (2002), for instance, addressed the question of which patch in a given habitat network ought to be enlarged to maximize metapopulation persistence. He varied the landscape structure and numerous species-ecological attributes, determined and characterized the "most promising" patch, and summarized his results in simple rules of thumb. The only shortcoming of his study is that the effect of a single patch is considered without taking the interplay with the other patches into account. Day and Possingham (1995) considered the patch size distribution as entirety. They addressed the question of whether equal-sized or variable-sized patches are better for metapopulation persistence. They varied the landscape structure, compared systems with and without migration but fixed the species' ecology, and derived rules of thumb. In neither study was the dispersal strategy varied.

All these examples indicate that they markedly contribute to a better understanding of the optimum patch size distribution but lack in the variation of important elements. This is not surprising because, in the past, studies of metapopulation persistence were dependent on numerical analyses of persistence measures. This of course limits the possibilities of systematic variation. Nowadays, however, we have an alternative. There are approximation formulas for the metapopulation capacity λ_M (Hanski and Ovaskainen 2000) and the mean lifetime T_m (Frank and Wissel 2002) - the measures for deterministic and stochastic metapopulation persistence. Formulas allow an analysis of their functional structure. In this way, important effects can be simply "read off", without numerical analysis work. The major advantage of the two formulas is that they provide insight into the interplay between landscape-structural and species-ecological attributes and its effect on metapopulation persistence. This gives rise to the hope that these possibilities can help to overcome the drawbacks in connection with the optimum patch size distribution.

In the following, we address the question of what patch size distribution is optimum for metapopulation persistence in a habitat network with a given number and configuration of patches. We present a systematic approach for the determination and analysis of optimum patch size distributions and the derivation of rules of thumb that is based on the formula T_m^a for the mean lifetime of metapopulations developed in Chapter 3 (Table 3.III). We reveal that the optimum patch size distribution can be determined by solving a simple system of linear equations. We give formulas for the optimum and uncover its functional dependence on the landscape structure (pattern of connectedness, patch configuration) and the species' ecology (various species-specific attributes, various dispersal strategies). On this basis, we derive rules of thumb and a "Principle of Optimality" which provide new insights into the optimum patch size distribution and the role of the species' dispersal strategy in this context. Finally, we draw some general conclusions on (a) the need to deduce simple, but ecologically differentiated rules of thumb and principles, and (b) the potential of using formulas such as T_m^a as tools for persistence analyses, theory building and management support. We finalize with some prospects for further research.

5.1 Methods

The present study has two objectives: Firstly, it aims at the determination and analysis of the optimum patch size distribution in a habitat network with a given patch configuration. Special emphasis is placed on a systematic investigation of the functional relationship between the optimum, the other spatial aspects of the habitat network (e.g. patch configuration, pattern of connectedness), and the species' ecology. Secondly, the study shall serve as a test of the formula for the mean lifetime of metapopulations, T_m^a, derived in Chapter 3. The formula ought to be tested regarding its ability to support metapopulation viability analyses and the derivation of tools for decision-support in habitat network design as well. This indicates which ingredients are needed for the study: the formula T_m^a, and appropriate submodels to integrate the landscape structure and the species' ecology.

Before we can turn to the formula and its submodels, however, we have to stress another point. Note that the formula for the mean lifetime T_m^a is based on the continuous time Markov chain model presented in Chapter 2. Hence, we have to specify a number of assumptions for the study in order to ensure that model and formula are really applicable.

5.1.1 Central assumptions

We consider *finite* metapopulations of N patches, take the *stochasticity* in the sequence of extinction and colonization events in to account, but *ignore Allee and rescue* effects. In this case, stochastic Levins-type models such as the model in Chapter 2 are applicable.

We focus on metapopulations which successfully approached *quasi-stationarity* before extinction, i.e. show typical fluctuations in the occupancy and go extinct with a constant rate. In this case, the mean lifetime T_m is known to summarize all the effects of the local and regional dynamics which are relevant for metapopulation persistence. This justifies to take T_m as currency in metapopulation viability analyses (remember Chapter 2).

We assume that the metapopulation does *not* consist of *multiple, isolated subnetworks.* In this case, the mean lifetime T_m is given by the negative reciprocal, $-1/\omega$, of the subdominant eigenvalue ω of the transition matrix A of the Markov model used (remember Chapter 2). This value is approximated by the formula T_m^a developed in Chapter 3.

To summarize, only if all these assumptions are met, the formula for the mean lifetime T_m^a is applicable and can be used for metapopulation viability analyses. In order to avoid an overloading of the present study with too many details, we additionally assume that the spatial correlation in the extinction events is negligible ($\rho_{ij} = 0$). For this case, a further simplified version of the lifetime formula T_m^a is available that is completely determined by the local extinction rates ν_i and the colonization rates c_{ij}.

5.1.2 The (simplified) formula for the mean lifetime T_m^a

In the uncorrelated case ($\rho_{ij} = 0$), the original formula T_m^a for the mean lifetime T_m of a metapopulation (see Chapter 3, Equation (3.20) and Table 3.III) simplifies to:

$$T_m^a = \frac{1}{\nu_{agg}} \cdot \frac{(N-1)!}{N \cdot (N-1)^{N-1}} \cdot e^{\frac{N}{(c_{tot}/\nu)_{agg}}} \cdot ((\frac{c_{tot}}{\nu})_{agg})^{N-1} \tag{5.1}$$

with

$$\nu_{agg} = \prod_{i=1}^{N} \nu_i^{\frac{1}{N}} \quad \text{and} \quad (\frac{c_{tot}}{\nu})_{agg} = \prod_{i=1}^{N} \max(\sqrt{2}, z_i)^{\frac{1}{N}} \tag{5.1a}$$

where

$$z_i = \frac{1}{\nu_i} \cdot \sqrt{\left(\tfrac{1}{2}\left((\textstyle\sum_{j(\neq i)} c_{ij})^{-2} + (\textstyle\sum_{j(\neq i)} c_{ji})^{-2}\right)\right)^{-1}}. \tag{5.1b}$$

Formula (5.1) essentially depends on the complex term z_i given by relation (5.1b). This term z_i is determined by the extinction rate ν_i of patch i and by two sums: $\sum_{j(\neq i)} c_{ij}$ and $\sum_{j(\neq i)} c_{ji}$. The first sum equals the total number of colonizations patch i can induce per time when occupied. The second sum equals the total probability that patch i becomes recolonized after an extinction and can be interpreted as a measure of "actually being in the play". Therefore, the term under the square root can be interpreted as the *effective* colonization rate of patch i. However, as the max-function in relation (5.1a) indicates, all these factors only contribute to $(\frac{c_{tot}}{\nu})_{agg}$ and, hence, to T_m if $z_i > \sqrt{2}$, i.e. if patch i is at least so strong that its effective colonization rate exceeds its local extinction rate by a factor of $\sqrt{2}$. Otherwise, this patch does not significantly contribute to T_m. This means that, as far as the persistence is concerned, the metapopulation effectively behaves as a metapopulation where all the ineffective patches are cancelled. In this study, all the analyses of metapopulation persistence will be carried out by using formula T_m^a (5.1).

In order to avoid a critical misuse of T_m^a, we should note that equation (5.1) reaches a limit of applicability if some of the patches become too small compared to other patches. In this case, the geometric mean ν_{agg} of the extinction rates overestimates the effect of the small patches and underestimates the resulting mean lifetime T_m of the metapopulation.

5.1.3 The submodels for including the landscape structure and the species' ecology

Last but not least, submodels are needed which relate the extinction rates ν_i and the colonization rates c_{ij} to the spatial structure of the habitat network and the to species' ecology. A habitat network is characterized by the patch locations (x_i, y_i), the patch sizes A_i, and the pattern of connectedness. Two patches i and j are said to be connected (short: $i \sim j$) if there is a corridor and some other linkage (e.g. visibility) between them.

5.1.3.1 Extinction rate

We use the following standard submodels for the local extinction rate:

$$\nu_i = \epsilon \cdot A_i^{-x} \tag{5.2}$$

(Goodman 1987; Foley 1994; Hanski 1994; Wissel *et al.* 1994; see also Chapter 2), where A_i is the size of patch i, ϵ a species-specific extinction parameter, and the power x a measure for the strength of environmental noise in the local population that summarizes both the strength of the fluctuations in essential environmental factors and the species' sensitivity to them. The stronger the environmental noise, the smaller the value of x.

5.1.3.2 Colonization rate

We use the following submodel for the colonization rate c_{ij} from patch i to patch j:

$$c_{ij} = \delta \cdot A_i \cdot a_{ij}, \tag{5.3}$$

where A_i is the size of patch i, δ the species-specific emigration rate per area unit, and a_{ij} the arrival probability, i.e. the probability that a disperser from patch i successfully reaches patch j (for a detailed ecological justification of the submodel, see Chapter 2). To integrate species dispersal, we use a variety of submodels for the arrival probability a_{ij} that cover a wide range of biologically reasonable dispersal strategies in patchy landscapes:

“Simple exponential” model

$$a_{ij} = e^{-\alpha \cdot d_{ij}}; \tag{5.3a}$$

“Pie-slice” model

$$a_{ij} = \frac{\sqrt{A_j}}{\pi^{3/2}} \cdot \frac{1}{d_{ij}} \cdot e^{-\alpha \cdot d_{ij}}; \tag{5.3b}$$

“Patch-oriented” model

$$a_{ij} = \frac{R(d_{ij})^{N-1}}{\sum_{k(\neq i)} R(d_{ik})^{N-1}} \cdot R(d_{ij}), \quad \text{where } R(d) = 1 - e^{-a \cdot e^{-b \cdot d}}; \tag{5.3c}$$

“Corridor-oriented” model

$$a_{ij} = \begin{cases} \frac{1}{n_i} \cdot e^{-\alpha \cdot d_{ij}} & \text{if } i \sim j \\ 0 & \text{else} \end{cases} . \tag{5.3d}$$

The term d_{ij} denotes the distance between two patches i and j and α^{-1} the species-specific dispersal range, i.e. the mean distance a disperser is able to cover. The function $R(d)$ is the so-called potential patch accessibility function (Heinz *et al.* 2004). Its two parameters a and b summarize the effects of the individuals' dispersal behavior that are relevant in the context of the arrival probability. Last but not least, term n_i denotes the total number of corridors adjacent to a certain patch i. The two first submodels are usually used to describe the effect of passive dispersal, whereas the latter two are relevant in connection with active dispersal (normal/correlated random walk or systematic search with the rule to stay at the first patch reached (5.3c); dispersal along corridors (5.3d)). All submodels depend on the patch configuration (patch-distances d_{ik}). Some additionally depend on the patch size A_j (see (5.3b)), or the pattern of connectedness (corridor configuration ($i \sim j$, n_i); see (5.3d)). For a detailed explanation of the four submodels, see Chapter 2.

5.1.3.3 Patch size distribution

To analyze the effect of the patch size distribution, we assume that a certain total habitat area A_{tot} is allocated over the patches according to a certain "allocation key" $(p_1, ..., p_N)$, where p_i is the proportion of habitat allocated to patch i. Then patch area A_i results from

$$A_i = p_i \cdot A_{tot}. \tag{5.4}$$

Although the submodels (5.2; 5.3; 5.4) take all the mentioned spatial aspects of habitat networks into account, they are still quite simple. There are only four species-ecological parameters $(\epsilon, x, \delta, \alpha)$ that must be considered. These submodels together with the equation for the mean lifetime (5.1) allow the effect of the patch size distribution on metapopulation viability to be analyzed, without having to run any simulation.

5.2 Results

The present study aims at determining the patch size distribution that is optimum for metapopulation persistence if a habitat network with a given number and configuration of patches is considered. A matter of particular interest is the extent to which the optimum depends on factors such as the patch configuration, the pattern of connectedness or the species' ecological attributes. We exclusively use the formula T_m^a (5.1) for the mean lifetime of metapopulations as tool for performing metapopulation viability analyses.

To derive general results regarding the effect of the landscape structure on metapopulation persistence is always a challenge because there is a lot of interaction between the patches that produces complexity. Hence, it seems to be almost impossible to solve the problem of determining the optimum patch size distribution in one step.

We use a hierarchical approach in order to enter this problem from the most simple side. In a first step, we perform a start-up analysis. The only aim of this step is to attain some hypotheses concerning the optimum allocation key. In a second step, we perform a systematic analysis of the functional structure of the formula T_m^a for the mean lifetime T_m in order to test the validity of the hypotheses concluded from the start-up analysis.

5.2.1 A start-up analysis

We consider a hypothetical habitat network with a certain number and a certain configuration of patches (see Table 5.I). We assume a species with "Corridor-oriented" dispersal, i.e. we use submodel (5.3d) for the arrival probability a_{ij}. We start with this dispersal strategy because it shows a medium degree of complexity (dependence of a_{ij} on patch configuration (d_{ij}) and pattern of connectedness ($\imath \sim j$)). Three random allocation keys (R1, R2, R3; see Table 5.I) are considered, each being determined by taking a random number from a uniform distribution between 0 and 1 for each component of the allocation key and normalizing them. These keys will be compared with three more systematic ones:

$$\textit{“Uniform”}: \; p_i = \tfrac{1}{N} \tag{5.5}$$

$$\textit{“Uneven”}: \; p_1 = \tfrac{1}{2}, \; p_i = \tfrac{1}{2(N-1)} \;\; \text{for all } i > 1 \tag{5.6}$$

$$\textit{“According to the degree of connectedness”}: \; p_i = \tfrac{n_i}{n_1+...+n_N} \tag{5.7}$$

The effect on metapopulation persistence is assessed by applying the submodels (5.2; 5.3; 5.4), inserting the outcome in formula (5.1), and calculating the value for the mean lifetime T_m. By comparing the resulting T_m-values for the different allocation keys under consideration, the most favorable one can be determined. This gives a rough idea about possible "candidates" for the optimum patch size distribution. In order to get an initial impression about the sensitivity of the optimum to factors such as the pattern of

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TABLE 5.I:

Positions (x, y) of the patches in the configuration shown in Figure 1 and three randomly generated allocation keys $(p_1, ..., p_8)$ denoted by "R1", "R2", "R3" for distributing the total habitat area A_{tot} over the patches, with p_i being the proportion of habitat allocated to patch i.

	1	2	3	4	5	6	7	8
x-coord	-1	0	0	0	0.5	1.5	3	3
y-coord	0	1	0	-2	-1	0.5	2.5	1
"R1"	0.17	0.13	0.21	0.09	0.06	0.19	0.04	0.11
"R2"	0.09	0.08	0.09	0.01	0.19	0.10	0.16	0.28
"R3"	0.04	0.13	0.27	0.26	0.04	0.10	0.12	0.04

connectedness or the species' ecology, we consider two patterns of connectedness (Figs. 5.1A-B) and compare the outcome for "weak" and for "strong" environmental noise. The results of this comparative analysis are displayed in Figures 5.1C-F. As can be seen, the question over what allocation key is best cannot be answered in general; the answer strongly depends on the total habitat area A_{tot} available. The larger the value of A_{tot}, the more the T_m-values for the various allocation keys differ. This again underlines the importance of knowing what sort of allocation is optimum. However, it can also be seen that, whenever A_{tot} is above a certain threshold value, a clear pattern can be identified. In the case of weak environmental noise (Figs. 5.1C-D), the "uniform" allocation key is found to be best, regardless of the pattern of connectedness. A totally different picture emerges if the environmental noise is strong (Figs. 5.1E-F). In this case, the allocation "according to the pattern of connectedness" is best. To summarize, the results of the start-up analysis give rise to the hypothesis that the optimum patch size distribution in a metapopulation depends on both the spatial structure of the pattern of connectedness and the strength of the environmental noise in the local populations (represented by parameter x) that depends on the environmental conditions and the species' response to them. But how reliable are these results? Do they show a certain generality or are they an effect of the particular landscape and the species considered in the start-up analysis?

5.2.2 How general are the results?

In the following, two main questions will be addressed: (a) Are the findings concerning the optimum patch size distribution robust against a change in the patch configuration or in the pattern of connectedness? (b) To what extent are the results affected by uncertainty in the species' ecological attributes summarized in the model parameters (x, ϵ, δ) and (α or a, b)? (c) What is happening if a species with another dispersal type is considered?

To answer these questions, we again make use of formula T_m^a. This formula gives insight into the interplay between the different factors and the effect on the mean lifetime T_m. Thus, we analyze its functional structure in the hope of obtaining an idea about the optimum patch size distribution in the general case and the effect of ecological uncertainty.

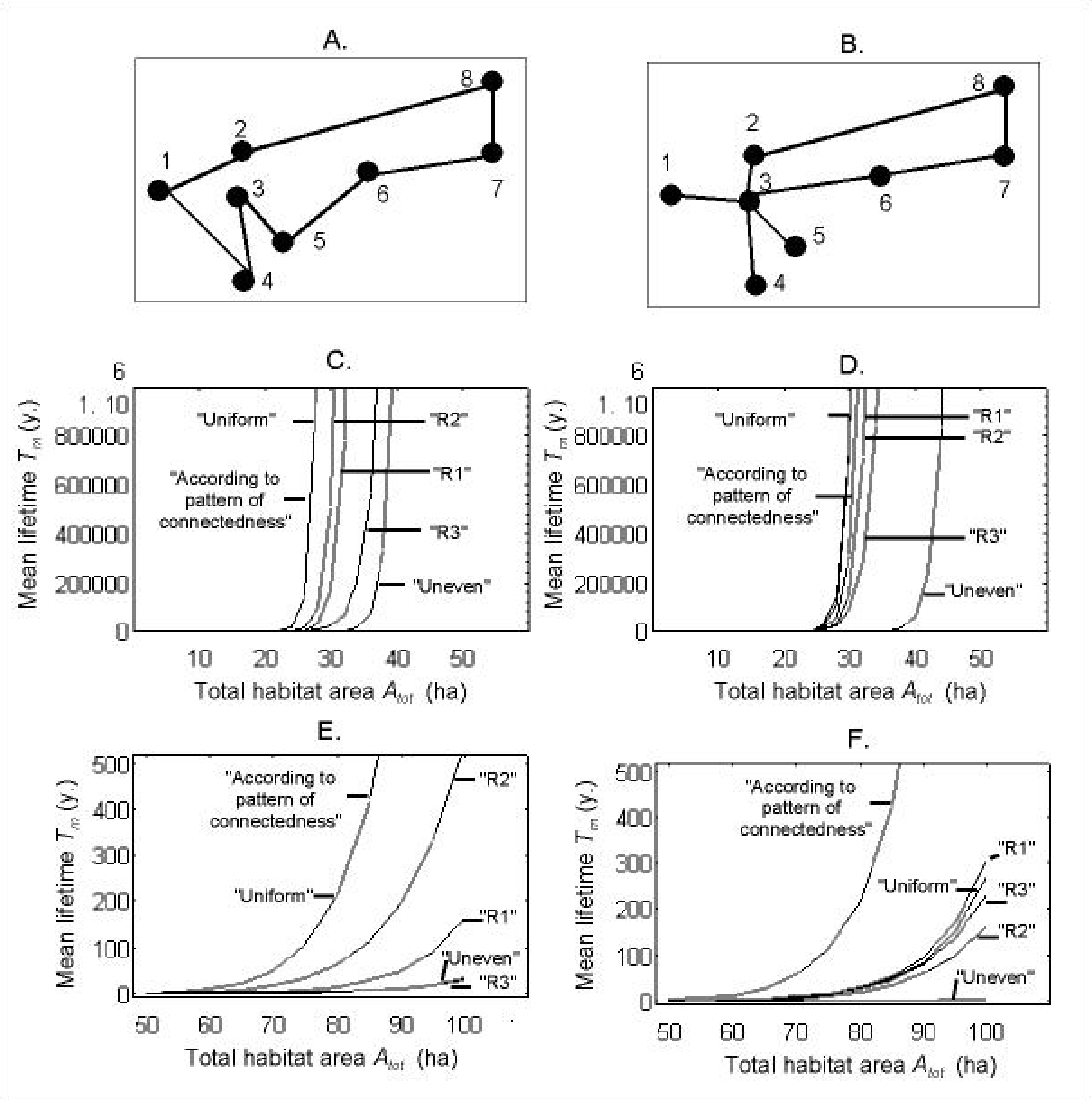

FIGURE 5.1: (A-B) The patch configuration and the patterns of connectedness considered in the start-up analysis (for the exact positions of the patches, see Table 5.I). (C-F) Mean lifetime of the metapopulation T_m calculated with equation (5.1) vs. total habitat area A_{tot} for the different allocation keys considered ("Uniform", "Uneven", "According to the pattern of connectedness", and "R1", "R2", "R3" given in Table 5.I) for weak environmental noise ($x = 2.5$; C-D) and strong environmental noise ($x = 0.5$; E-F). All the other parameters used are: $\epsilon = 1, \delta = 1, \alpha = 1$.

For the following analysis, however, we assume that the total habitat area A_{tot} is so large that the following two conditions are met: (a) Each patch in the considered habitat network really contributes to metapopulation persistence. This condition means that $z_i > \sqrt{2}$, i.e. the ratio z_i between the effective colonization rate and the local extinction rate for each patch i (see relation (5.1b)) exceeds the critical value of $\sqrt{2}$. This simplifies the aggregated term $(\frac{c_{tot}}{\nu})_{agg} = \prod_{i=1}^{N} z_i^{1/N}$ that is now given by a usual geometric mean of the z_i's (see relation (5.1a)). (b) A_{tot} is so large that $(\frac{c_{tot}}{\nu})_{agg} > N-1$ with the consequence that $e^{\frac{N-1}{(c_{tot}/\nu)_{agg}}} \approx 1$. If both conditions are met then formula (5.1) can be further simplified and expressed as a product of three components:

$$\begin{aligned} T_m^a \;\approx\; & \left(\prod_{i=1}^{N} \frac{1}{\nu_i}^{\frac{1}{N}}\right)^{N} \cdot \frac{(N-1)!}{N(N-1)^{N-1}} \\ & \times \left(\prod_{i=1}^{N} \sqrt{\left(\frac{1}{2}\left((\sum_{j(\neq i)} c_{ij})^{-2} + (\sum_{j(\neq i)} c_{ji})^{-2}\right)\right)^{-1}}^{\frac{1}{N}}\right)^{N-1} \end{aligned} \tag{5.8}$$

5.2.2.1 Analyzing the first part

The first part of equation (5.8) is given by the mean lifetimes $T_i = 1/\nu_i$ of the local populations and is summarizing all the extinction effects on metapopulation persistence. By inserting the submodel for the extinction rates $\nu_i = \epsilon {A_i}^{-x}$ into this term, we get

$$\prod_{i=1}^{N} \frac{1}{\nu_i}^{\frac{1}{N}} = \frac{1}{\epsilon} \cdot \left(\prod_{i=1}^{N} A_i^{\frac{1}{N}}\right)^{x} \tag{5.9}$$

that mainly consists of a usual geometric mean of the patch areas A_i. It is well-known from mathematics that a geometric mean takes its maximum at a uniform distribution. Therefore, we can conclude that relation (5.9) maximizes if the total habitat area A_{tot} is uniformly distributed over the N patches, i.e. $A_i = \frac{1}{N} \cdot A_{tot}$.

5.2.2.2 Analyzing the second part

The second part of equation (5.8) only depends on the number of patches N in the metapopulation under consideration. Therefore, it only gives a pre-factor that does not influence the optimum patch size distribution.

5.2.2.3 Analyzing the third part

The third part of equation (5.8) is completely determined by the colonization rates c_{ij}. It summarizes all the colonization effects on metapopulation persistence. Two terms are found to be of special importance: the total rate of colonizing any other patch, $\sum_{j(\neq i)} c_{ij}$, and the total rate of becoming recolonized after an extinction, $\sum_{j(\neq i)} c_{ji}$. Relation (5.8) indicates that a quadratic harmonic mean of the two terms is decisive for T_m. As is known from mathematics, a quadratic harmonic mean $\sqrt{(\frac{1}{2}(x^{-2}+y^{-2}))^{-1}}$ of two numbers x and y maximizes if $x = y$. Therefore, the third part of equation (5.8) maximizes if

$$\sum_{j(\neq i)} c_{ij} = \sum_{j(\neq i)} c_{ji} \qquad \text{for all } i \in \{1, ..., N\}, \tag{5.10}$$

i.e. there is a balance between "colonizing" and "becoming recolonized". By inserting the submodel $c_{ij} = \delta \cdot A_i \cdot a_{ij}$ for the colonization rates c_{ij} (5.3), we find that balance condition (5.10) is only met if the patch areas A_i solve the following system of linear equations:

$$\delta \cdot A_i \cdot (\sum_{j(\neq i)} a_{ij}) = \delta \cdot \sum_{j(\neq i)} A_j \cdot a_{ji} \qquad \text{for all } i \in \{1, ..., N\}. \tag{5.11}$$

Evidently, this relation can be re-written in matrix form:

$$\begin{pmatrix} -(\sum_{j(\neq 1)} a_{1j}) & a_{21} & \cdots & a_{N1} \\ a_{12} & -(\sum_{j(\neq 2)} a_{2j}) & \cdots & \vdots \\ \vdots & \vdots & \ddots & \vdots \\ a_{1N} & \cdots & \cdots & -(\sum_{j(\neq N)} a_{Nj}) \end{pmatrix} \cdot \begin{pmatrix} A_1 \\ \vdots \\ \vdots \\ A_N \end{pmatrix} = \begin{pmatrix} 0 \\ \vdots \\ \vdots \\ 0 \end{pmatrix}. \tag{5.12}$$

Note that the non-diagonal entries of the matrix M are non-negative (since $m_{ij} = a_{ji} \geq 0$) and the sum over the entries m_{ji} of each column i is zero (since $m_{ii} = -\sum_{j(\neq i)} m_{ji}$). Hence, matrix M is a stochastic generator and the vector of the patch areas $(A_1, .., A_N)$ has to be its zero-solution. It is well-known from Perron-Frobenius theory (Minc 1988) that stochastic generator matrices have a uniquely determined (up to scaling factors), positive zero-solution $\mathbf{q} = (q_1, .., q_N) > 0$, provided the matrix is irreducible. This can be assumed in our case because reducibility would result if the habitat network would consist of isolated subnetworks, that is excluded. Hence, relations (5.10; 5.11; 5.12) are solved if

$$A_i = \frac{q_i}{\sum_{k=1}^{N} q_k} \cdot A_{tot} \qquad \text{for all } i \in \{1, ..., N\}, \tag{5.13}$$

i.e. the patch areas A_i are allocated according to the components q_i of the zero-solution $\mathbf{q}$ of matrix M. This solution is completely determined by the arrival probabilities a_{ij}. Its existence and uniqueness are independent of the details of the underlying dispersal processes. Hence, the question over when the third part of equation (5.8) maximizes can always be answered in a unique manner. Once the the arrival probabilities a_{ij} are specified by the mean of empirical data or any appropriate submodel, standard algorithms allow the zero-solution $\mathbf{q}$ of the corresponding matrix M and so the allocation key (5.13) to be determined (e.g. using algebraic calculation programs such as Mathematica or MathLab).

Now we pass on to the submodel for a_{ij} used in the start-up analysis. We assumed "Corridor-oriented" dispersal, i.e. we used submodel (5.3d). Hence, the system to be solved is $\frac{A_i}{n_i} \cdot (\sum_{j(\sim i)} e^{-\alpha \cdot d_{ij}}) = \sum_{j(\sim i)} \frac{A_j}{n_j} \cdot e^{-\alpha \cdot d_{ji}}$. It is solved if $A_i = \frac{n_i}{n_1 + \ldots + n_N} \cdot A_{tot}$, i.e. the total habitat area A_{tot} is distributed according to the number of corridors n_i adjacent to the individual patches i, regardless of the patch configuration (note that $d_{ij} = d_{ji}$).

5.2.2.4 Consequences for the behavior of the entire formula T_m^a

Evidently, the different parts of equation (5.8) maximize at different allocation keys. Whereas the first part becomes maximum if $p_i = \frac{1}{N}$, the third part maximizes if $p_i = \frac{n_i}{n_1 + \ldots + n_N}$. But what does this mean for the entire equation (5.8)? In order to answer this question, we can make use of another effect. As the relations (5.9) and (5.11) indicate, the first part is proportional to ${A_{tot}}^x$, whereas the third part is proportional to A_{tot}. This allows us to conclude the following: If the environmental noise in the local populations is weak (i.e. x is markedly > 1) then the first part dominates equation (5.8). Hence, T_m^a maximizes if $A_i = \frac{1}{N} \cdot A_{tot}$. But if the environmental noise in the local population is strong (i.e. x is markedly < 1) then the third part is decisive. Therefore, T_m^a maximizes if $A_i = \frac{n_i}{n_1 + \ldots + n_N} \cdot A_{tot}$. These findings confirm the results of the start-up analysis.

5.2.2.5 Robustness of the results against ecological uncertainty

So far, we have only analyzed the effect of the strength of the environmental noise in the local populations (parameter x) on the optimum patch size distribution. But what about the effect of the other species' parameters, in particular (ϵ, δ)? What is happening if another dispersal type is considered? In order to answer these questions, we completely express the lifetime formula T_m^a in terms of the patch areas (A_i), the arrival probabilities (a_{ij}) and the species' ecological attributes (x, ϵ, δ). By inserting our submodels for the extinction rates ν_i (5.2) and for the colonization rates c_{ij} (5.3) in relation (5.8), we get

$$\begin{aligned} T_m^a &= \frac{1}{\epsilon}\left(\frac{\delta}{\epsilon}\right)^{N-1} \cdot \frac{(N-1)!}{N(N-1)^{N-1}} \cdot \left(\prod_{i=1}^{N} A_i\right)^{x} \\ &\times \left(\prod_{i=1}^{N} \sqrt{\left(\frac{1}{2}\left((\sum_{j\neq i} A_i \cdot a_{ij})^{-2} + (\sum_{j\neq i} A_j \cdot a_{ji})^{-2}\right)\right)^{-1}}\right)^{\frac{N-1}{N}} \end{aligned} \tag{5.14}$$

This relation indicates that the parameters ϵ and δ only determine a pre-factor of formula T_m^a which actually influences the value of the mean lifetime T_m, but does not have any effect on the relative results. This means that uncertainty in ϵ or δ is uncritical because it does not affect the ranking orders among the alternative scenarios considered. Hence, the only critical source of uncertainty in the species-ecological attributes is the strength of environmental noise in the local populations (parameter x). It is certainly almost impossible to determine the exact value of x. But as we have seen, a high "precision" is anyway not needed. It is sufficient to know whether the environmental noise in the local populations under consideration is weak ($x > 1$) or strong ($x < 1$). By using the structural information that $x = \frac{2r}{\sigma^2} - 1$ (Goodman 1987; Foley 1994; Wissel *et al.* 1994) with r being the mean and σ^2 the variance of the local populations' reproduction rates, this rough estimation is certainly easier to obtain than hard data.

In order to avoid a misunderstanding about the role of the parameters (ϵ, δ), we should note the following: The whole study was based on the assumption that the total habitat area A_{tot} is large enough to ensure that all patches can significantly contribute to metapopulation persistence ($z_i > \sqrt{2}$). What value of A_{tot} is needed to meet this condition depends on ϵ, and δ (see relations (5.1b, 5.2, 5.3)).

To clarify the role of the dispersal type, we take the other submodels for the arrival probabilities a_{ij} ("Simple exponential" (5.3a), "Pie-slice" (5.3b), and "Patch-oriented" (5.3c)), determine the zero-solutions $\mathbf{q}$ for the corresponding matrices M (see (5.12)), and calculate the resulting allocation keys using (5.13). The calculations for the different dispersal types are done in the Appendix. They lead to the following results:

Dispersal model	*Optimum patch size distribution*
"Simple exponential"	$A_i = \frac{1}{N} \cdot A_{tot}$
"Pie-slice"	$A_i = \frac{1}{N} \cdot A_{tot}$
"Corridor-oriented"	$A_i = \frac{n_i}{n_1+..+n_N} \cdot A_{tot}$
"Patch-oriented"	$A_i = \frac{\sum_{k(\neq i)} R(d_{ik})^{N-1}}{\sum_j \sum_{k(\neq j)} R(d_{jk})^{N-1}} \cdot A_{tot}$,

where $R(d) = 1 - e^{-a \cdot e^{-b \cdot d}}$ is the potential patch accessibility function. The list highlights an important effect. It indicates that the optimum patch size distribution depends on the dispersal model used. In the first two cases ("Simple exponential" and "Pie-slice"), a uniform distribution is found to be optimum, whereas in the other two cases, the optimum is found to depend on the landscape structure. In the "Corridor-oriented" case, the pattern of connectedness (n_i) is decisive, whereas the patch configuration (d_{ij}) and the concrete dispersal behavior do not matter. In the "Patch-oriented" case, however, the total potential accessibility $\sum_{j(\neq i)} R(d_{ij})^{N-1}$ of the individual patches i and, hence, the number (N) and configuration (d_{ij}) of the patches as well as the individuals' movement behavior (condensed in a and b) are crucial. In the case of larger patch numbers N, the latter allocation key can be further simplified. If $R_{max} = \max(R(d_{ik}) : i, k)$ denotes the maximum potential patch accessibility attainable in the habitat network then we obtain

$$\frac{\sum_{k(\neq i)} R(d_{ik})^{N-1}}{\sum_j \sum_{k(\neq j)} R(d_{jk})^{N-1}} = \frac{\sum_{k(\neq i)} \left(\frac{R(d_{ik})}{R_{max}}\right)^{N-1}}{\sum_j \sum_{k(\neq j)} \left(\frac{R(d_{jk})}{R_{max}}\right)^{N-1}} \approx \frac{\tilde{n}_i}{\tilde{n}_1 + .. + \tilde{n}_N}, \tag{5.15}$$

where $\tilde{n}_i$ denotes the number of patches k for which $R(d_{ik}) \approx R_{max}$, i.e. which belong to the "nearest neighbors" of patch i. To understand the latter step, note that $\left(\frac{R(d_{ik})}{R_{max}}\right)^{N-1} \approx 1$ if $R(d_{ik}) \approx R_{max}$ and $\left(\frac{R(d_{ik})}{R_{max}}\right)^{N-1} \approx 0$ if $R(d_{ik}) < R_{max}$ for larger values of N. This indicates that the allocation key approaches the rule "Allocate according to the number $\tilde{n}_i$ of the nearest neighbors". Note the similarity to the rule for the "Corridor-oriented" case.

How can this mathematical result be interpreted in ecological terms? Note that the first two dispersal models ("Simple exponential", "Pie-slice") are characterized by a lack of any "competition" between the patches for dispersers (arrival probability a_{ij} at patch j is not influenced by any other patch k). In the latter two cases ("Corridor-oriented", "Patch-oriented"), however, the situation is completely different. The corresponding models assume a certain total number of emigrants per patch which are "influenced" in their decision to start towards one or another patch. In the Corridor-oriented case, the decision is influenced by the corridors adjacent to start patch i. Hence, all the patches j with corridor-connection to patch i out-compete all the patches k without such a connection. In the other case, the dispersers stay at the first patch they reach. This prevents them from continuing to any other patch. Both mechanisms result in a competition effect. Our results indicate that the optimum patch size distribution strongly depends on whether or not the species' dispersal strategy causes a competition effect and on the nature of this effect as well (which landscape elements have an attracting influence on the dispersers (e.g. adjacent corridors, nearest neighbor patches)?). Once the dispersal strategy of a given species is characterized in this sense, the optimum allocation key can be concluded.

To summarize, just by analyzing the functional structure of formula T_m^a (equation (5.8)), we were able to confirm the results of the start-up analysis. Moreover, we could simply "read-off" all the critical sources of ecological uncertainty.

5.2.3 Derivation of tools for habitat network design

The presented analysis reveals a clear pattern regarding the optimum patch size distribution in the case that the total habitat area A_{tot} is large enough to ensure that all the patches in the habitat network under consideration can significantly contribute to metapopulation persistence. By taking the findings as a basis, we can go a step further and derive tools which provide a rough orientation for habitat network design.

5.2.3.1 Rules of thumb for optimum patch size distribution

As we have seen, the optimum patch size distribution strongly depends on two factors: (a) the strength of environmental noise in the local populations (parameter x) that summarizes the environmental conditions and the species' response to them, and (b) the species' dispersal strategy. The following rules of thumb can be formulated:

Rule 1: If the environmental noise in the local populations is weak ($x < 1$) then metapopulation persistence is maximum if all patches are nearly of the same size, i.e. $A_i \approx A_j$, irrespective of the species' dispersal strategy.

Rule 2: If the environmental noise in the local populations is strong ($x > 1$) then metapopulation persistence is maximum if the size of the patches A_i corresponds to their "competitiveness" DC_i (competition for dispersers), i.e. $\frac{A_i}{A_j} \approx \frac{DC_i}{DC_j}$. The competitiveness DC_i depends on the landscape structure and the species' dispersal strategy:

- Passive dispersal: $DC_i = const = 1$ (equal competitiveness);
- Corridor-oriented dispersal: $DC_i = n_i$ (number of adjacent corridors);
- Patch-oriented dispersal (large N): $DC_i = \tilde{n}_i$ (number of nearest neighbors);
- Patch-oriented dispersal (small N): $DC_i = \sum_k R(d_{ik})^{N-1}$ (total accessibility).

Both rules recommend supporting the entire habitat network instead of supporting a particular patch. These recommendations, however, depend on our assumption that the total habitat area A_{tot} is so large that a certain minimum exchange between the patches is ensured. It is known that, in this case, the habitat network has an advantage over a single large patch (e.g. Day and Possingham 1995; Stacey *et al.* 1997; Drechsler and Wissel 1998). If A_{tot} is smaller than required then the rules of thumb presented lose their validity.

The finding in the case of "weak noise" that the optimum patch size distribution is independent of both patch configuration and pattern of connectedness is a reflection of the fact that the metapopulation first of all benefits from its long-term persistent local populations. This also agrees with the rule of thumb of Etienne and Heesterbeek (2001).

With "strong noise", the situation is slightly different. Here, the local populations are short-term persistent and the metapopulation depends on successful recolonizations. Hence, factors relevant for colonization become increasingly important. The optimum patch size distribution indicates that, in this case, it is best for metapopulation persistence if the patch size distribution tallies with the pattern of competitiveness that depends on landscape structure (pattern of connectedness/patch configuration) and dispersal strategy.

The two rules presented correspond with the rule of thumb by Day and Possingham (1995). Day and Possingham showed that a habitat network with equal-sized patches is better for metapopulation persistence than a habitat network with variable-sized patches, irrespective of the strength of environmental noise in the local populations. Their analysis was based on a dispersal model without any competition term.

At first sight, it appears surprising that the optimum patch size distribution is independent of the patch configuration in case of passive or corridor-oriented dispersal. Undoubtedly, patches with an above-average closeness to their neighbors can contribute to metapopulation persistence with above-average effectiveness and so need to be enlarged first. But note that there is also a need to make an "investment" in all the other patches. Patches with below-average closeness to their neighbors must be enlarged in order to ensure that these patches can significantly contribute to metapopulation persistence at all. The need to support the habitat network as a whole is a consequence of the fact that the stochasticity in the sequence of extinction and colonization events is taken into account. The larger the number of strong patches in the habitat network, the better the negative effect of this stochasticity can be counteracted (see also Frank (2005) and Chapter 6).

5.2.3.2 A "Principle of Optimality"

In the case of strong environmental noise, the local populations are only short-term persistent, and so the metapopulation strongly depends on successful colonization events. This well-known effect is reflected by the fact that the mean lifetime T_m is dominated by the third part of relation (5.8). As our study reveals, this part (and, hence, T_m) maximizes if

$$\sum_{j(\neq i)} c_{ij} = \sum_{j(\neq i)} c_{ji} \quad \text{for all } i \in \{1, ..., N\}, \tag{5.16}$$

i.e. a certain balance between "colonizing" and "becoming recolonized" is ensured. This balance condition can be interpreted as "Principle of Optimality" for metapopulation persistence for the case of strong environmental noise. This principle reveals that a certain management measure can only effectively support metapopulation persistence if both sides of the "colonization coin" are supported. A frequently colonized sink patch is thus as ecologically ineffective as a too rarely recolonized source patch.

As relation (5.16) indicates, the Principle of Optimality is exclusively formulated in the language of the colonization rates c_{ij}. This shows that the optimum patch size distribution can simply be determined by solving the system of equations (5.16) in the general case, even if the functional relationship between the rate of colonization c_{ij} and patch area A_i is different from that given by submodels (5.3 and 5.3a-d) used here.

To summarize, neither the two rules of thumb nor the Principle of Optimality provide a detailed guideline for metapopulation management in any specific case. Both tools, however, give a rough orientation. Knowing the optimum patch size distribution as described by the rules of thumb is sometimes useful for decision-making, even if it is certain that the optimum itself cannot be reached. The optimum provides a reference for setting correct management priorities (which of a variety of possible alternative measures will bring the system closest to the optimum?). The principle of optimality draws the decision-maker's attention to an important metapopulation dynamic effect. It points out that the balance between "colonizing" and "becoming recolonized" becomes a key factor of effectiveness of metapopulation management if the environmental noise in the local populations is strong.

5.3 Discussion

By analyzing the functional structure of the formula T_m^a for the mean lifetime (equation (5.1)), we were able to derive formulas and rules of thumb for the optimum patch size distribution in metapopulations with given patch configurations and to deduce a "Principle of Optimality" as well. Formulas, rules and principle are valid for classes of species (see Section 5.2.3.1). They generalize existing rules of thumb such as those by Day and Possingham (1995) or Etienne (2002). By comparing the results for the different classes, new insights about the optimum patch size distribution in metapopulations and the role of the species' dispersal strategy in this context can be obtained, as is explained below.

The results of this study also give rise to some conclusions about the chance of finding general laws in population ecology – a question that is widely discussed in recent ecology (Berryman 1999; Lawton 1999; Murray 2000; Turchin 2000) and has implications for both theory and practical conservation. By taking the rules of thumb and the presented principle of optimality as a basis, we discuss the limits of generality of laws in the field of metapopulation persistence and habitat network design. Moreover, we discuss the potential of using formulas like T_m^a as tools for persistence analyses to the benefit of theory building and management support. Finally, we give some prospects for further research.

5.3.1 New insights into the optimum patch size distribution

As we have seen, the question of what patch size distribution is optimum for metapopulation persistence cannot be answered in general. Depending on the type of the considered species, a uniform or a network-dependent distribution can be optimum. Various aspects of the network structure can be determinant for the optimum patch size distribution: the pattern of connectedness, the nearest neighbors, or the entire patch configuration.

The preceding findings also give insight into the effect of patch size variability on metapopulation persistence (Anderson 1991; Hanski and Gyllenberg 1993; Hanski 1994; Day and Possingham 1995; Ovaskainen and Hanski 2003; Frank 2005). They indicate that patch size variability is only favorable for metapopulation persistence if the following two conditions are met: (a) The considered species shows strong environmental noise in the local populations and has a dispersal strategy that induces competition between the patches for dispersers, and (b) The "right" patches are above-average large. The latter condition is a reflection of the fact that, in the case of dispersal with competition effect, the patch size distribution has to tally with a certain other spatial aspect of the habitat network (network-dependent optimum!). Which aspect is relevant depends on the species' dispersal strategy. Note, however, that the whole study was based on the assumption of having significant exchange between the patches. With decreasing exchange, the relative importance of patch size variability increases (see also Day and Possingham 1995).

The decisive criterion for the optimum patch size distribution was the competitiveness of the patches (Rule 2 in Section 5.2.3.1). Evidently, the competitiveness/attrativeness of a patch influences the number of immigrants and so the chance of becoming recolonized after an extinction. Hence, the rule "allocate habitat according to the competitiveness" ensures that the colonization ability of a patch tallies with its recolonization chance. This corresponds with the intention of the Principle of Optimality presented. This is not surprising because the derivation of Rule 2 started from the Principle (system (5.16)). Therefore, Rule 2 can be interpreted as tool for implementing the general Principle.

5.3.2 Key factor "competition effect"

One central element of the presented analysis was the comparison of four dispersal models. This allowed us to attain better insight into the relationship between the optimum patch size distribution and the species' dispersal strategy. We see that the species' dispersal strategy crucially influences the optimum patch size distribution, but only as long as the environmental noise in the local populations is strong and the metapopulation depends on successful colonization events. But our results also reveal that the dispersal strategy only matters if it induces competition between the patches for dispersers. This indicates that the *actual key factor* for the optimum patch size distribution is the *competition effect*.

What does the competition effect cause? In the absence of any competition effect, the uniform patch size distribution is optimum. This particularly indicates that the optimum patch size distribution is independent of the spatial structure of the habitat network. In the presence of a competition effect, however, an additional interaction between the patches comes into play which primarily influences the immigration rates. This additional interaction changes the entire spatiotemporal dynamics of the metapopulation and so the functional relationship between the landscape structure and metapopulation persistence. One implication is that the uniform patch size distribution is not optimum anymore. Instead of, a certain network-dependent distribution becomes optimum. The nature of the competition effect (e.g. caused by corridor-orientation or patch-orientation) determines which spatial aspect of the network structure is decisive for the optimum patch size distribution (e.g. pattern of connectedness, patch configuration). Last but not least, the network-dependence of the optimum reveals that, in presence of a competition effect, a certain correspondence between the patch size distribution and the network structure is required for metapopulation persistence. All these arguments show that the optimum patch size distribution is highly sensitive to the absence or presence of any competition effect.

A high sensitivity of spatial effects to the absence or presence of competition between patches for dispersers has also been found in connection with another aspect of metapopulation persistence. Heinz *et al.* (submitted) considered alternative habitat networks and ranked them according to their effect on metapopulation persistence (measured in terms of T_m). They reported a high sensitivity of the ranking orders to changes in the details of the individuals' dispersal behavior. All the dispersal patterns they analyzed were of the "Patch-oriented" case, i.e. induced a competition effect. After artificially excluding the competition effect, however, high robustness of the ranking orders against changes in the dispersal behavior was found. This shows that all the reported behavioral effects on the ranking orders primarily worked over the competition effect.

The two studies indicate that the mentioned competition effect is crucial in the analysis of landscape effects on metapopulation persistence. Therefore, it must not be ignored, otherwise there is a high risk of counter-productive conclusions. This indicates the need to check every dispersal strategy for the emergence of competition effects. Whether individual movement is oriented and to which sort of landscape elements is certainly easier to determine than detailed movement patterns.

5.3.3 Ecologically differentiated rules and principles are needed

Two tools have been derived which condense important effects of metapopulation persistence and provide a rough orientation for habitat network design: rules of thumb for the optimum patch size distribution and a Principle of Optimality. Both tools, however, are not valid in general. Different ecological cases must be distinguished: weak and strong environmental noise in the local populations; dispersal strategies with and without competition effect ("competition" between the patches for dispersers).

This reveals a dilemma of the classical neutral rules of thumb of the type "One large is better than several small" or "The closer, the better" found in many textbooks on landscape ecology (e.g. Wilson and Willis 1975; Wilcove *et al.* 1986). On the one hand, these rules try to condense important functional relationships between landscape structure and species' survival in an as simple as possible way. This is important for conservation practice, because overly complex rules would never be applied. On the other hand, these rules completely ignore differences in the species' ecology. This over-simplification is critical because it can lead to counter-productive decisions, at least for some species.

The present study shows that there is a good chance of overcoming this drawback by formulating ecologically differentiated but still simple rules of thumb of the type "If the species is of type X, then the optimum is Y". At a first glance, managing the diversity of the species' ecological attributes seems hopeless. But as is well-known from numerous population viability analyses, relative results are usually extremely robust to change in the species' ecological attributes (e.g. Lindenmayer and Possingham 1996; Drechsler *et al.* 2002). Only a few attributes are usually found to have an influence on the relative results - and hence on the optimum - at all (in our case, strength of environmental noise x, type of dispersal). Only these attributes have to be taken as a basis for classifying the species. After determining the functional relationship between the decisive attributes and the optimum, rules of thumb of the mentioned type can be formulated. These rules are valid for whole ecological classes of species (see also Verboom *et al.* (1993), Frank and Wissel (1998), and the concept of "ecological profiles" by Weaver *et al.* (1996)). This has strong implications for conservation management. Firstly, it allows the focal point of conservation to be shifted from a particular target species to a class of species of a certain type. Secondly, although ecologically differentiated rules of thumb cannot solve the conflict concerning what type of species should be supported, they allow the consequences of a planned management measure to be assessed through the eyes of all the species considered. In this way, decisions can be made on a more scientifically sound basis.

5.3.4 On the practical value of formulas like T_m^a for decision-support in conservation management

All the analysis work in the present study was exclusively carried out by the mean of the formula T_m^a for the mean lifetime of a metapopulation given by equation (5.1). This formula allows decision-making in the context of habitat network design to be supported in several respects. Firstly, the formula shows how data from species and landscape have to be combined to *predict* the resulting metapopulation viability. In this way, alternative scenarios can be quantitatively assessed, compared, and ranked according to their effect on metapopulation persistence. Secondly, the functional structure of the formula provides insight into the interplay between landscape structure and species' ecology and its consequences for metapopulation dynamics. This improves *understanding* and is certainly the main advantage of the formula. In particular, important metapopulation dynamical effects such as the Principle of Optimality presented can simply be "read off". Thirdly, the formula allows the robustness of the relative results to ecological *uncertainty* to be assessed. By analyzing its functional structure, it can be determined what species-ecological attributes affect ranking orders and optimum values in the first place. In consequence, ecologically differentiated rules of thumb can be derived. All these findings reveal that analyzing formulas like T_m^a is a useful approach if rules of thumb or general principles of (meta)population persistence need to be derived.

5.3.5 Prospects for further research

The assumptions underlying the present study show some prospects for further research: (a) The presented rules of thumb depend on the assumption that the total habitat area A_{tot} exceeds a certain minimum. Therefore, both an estimate of the critical minimum and rules of thumb for the case that A_{tot} is below this threshold are needed. (b) In order to cover a wider range of ecological situations, it has to be analyzed how the presented rules of thumb change if Allee or rescue effects are taken into account. (c) In the present study, stochastic metapopulation dynamics are considered and the formula T_m^a for the mean lifetime of metapopulations of Frank and Wissel (2002) is taken as a measure of persistence. In the case of deterministic metapopulation dynamics, there are other measures of persistence such as the metapopulation capacity λ_M by Hanski and Ovaskainen (2000), or the basic reproduction ratio R_0 by Etienne and Heesterbeek (2000). Therefore, it is useful to compare the optimum patch size distributions resulting from the different measures. This reveals how robust the rules of thumb are to a change in the measure of persistence and how strongly they depend on the assumption of considering deterministic or stochastic dynamics (see Chapter 6). (d) Because of the practical value of having landscape measures for population persistence, it is useful to develop techniques for deriving approximation formulas for the output of any spatially realistic PVA model (see Chapter 9).

5.4 Appendix

Determination of the optimum allocation key for the remaining dispersal models ("Simple exponential" (5.3a), "Pie-slice" (5.3b), "Patch-oriented" (5.3c))

To determine the optimum allocation key $\mathbf{q} = (q_1, .., q_N)$ for the distribution of a given total amount of habitat A_{tot} over a given habitat network means to determine the zero-solution of the stochastic generator matrix M specified in (5.12). The central step towards a solution for the three dispersal models under consideration is the following relationship that is well-known from matrix theory: if the arrival probabilities a_{ij} are *symmetric*, i.e. $a_{ij} = a_{ji}$ for all $i \neq j$, then M is symmetric as well and $\mathbf{1} = (1, .., 1)$ is the zero-solution of M (Minc 1988). Now we pass on to the three dispersal models of interest.

Simple exponential.– Evidently, the arrival probabilities $a_{ij} = e^{-\alpha \cdot d_{ij}}$ are per definition symmetric. Hence, $\mathbf{q} = \mathbf{1}$ and the optimum patch size distribution is given by $A_i = \frac{1}{N} \cdot A_{tot}$.

Pie-slice.– In the case of the Pie-slice model $a_{ij} = \frac{\sqrt{A_j}}{\pi^{3/2}} \cdot \frac{1}{d_{ij}} \cdot e^{-\alpha \cdot d_{ij}}$, the situation is more complex. But note that $A_i \cdot a_{ij} \equiv \tilde{A}_i \cdot \tilde{a}_{ij}$ with $\tilde{A}_i = \sqrt{A_i}$ and $\tilde{a}_{ij} = \sqrt{A_i} \cdot a_{ij} = \frac{\sqrt{A_i \cdot A_j}}{\pi^{3/2}} \cdot \frac{1}{d_{ij}} \cdot e^{-\alpha \cdot d_{ij}}$. Consequently, if vector $(A_1, .., A_N)$ solves (5.12) for the original values a_{ij} then vector $(\tilde{A}_1, .., \tilde{A}_N)$ solves (5.12) for the transformed values $\tilde{a}_{ij}$, and vice versa. Evidently, the $\tilde{a}_{ij}$-values are symmetric. Hence, $\mathbf{q} = \mathbf{1}$, i.e. the $\tilde{A}_i$-values ought to be uniformly distributed and so the values of $A_i (= \tilde{A}_i^2)$ as well. This gives $A_i = \frac{1}{N} \cdot A_{tot}$.

Patch-oriented.– Here, we can use the same "trick" as in the preceding case. The arrival probabilities are given by $a_{ij} = \frac{R(d_{ij})^{N-1}}{\sum_{k(\neq i)} R(d_{ik})^{N-1}} \cdot R(d_{ij})$. Evidently, $A_i \cdot a_{ij} \equiv \tilde{A}_i \cdot \tilde{a}_{ij}$ with $\tilde{A}_i = \frac{A_i}{\sum_{k(\neq i)} R(d_{ik})^{N-1}}$ and $\tilde{a}_{ij} = R(d_{ij})^N$. As before, the $\tilde{a}_{ij}$-values are symmetric and so the $\tilde{A}_i$-values ought to be uniformly distributed. But note the $\tilde{A}_i = const = c$ implies that $A_i = c \cdot \sum_{k(\neq i)} R(d_{ik})^{N-1}$. Consequently, $A_i = \frac{\sum_{k(\neq i)} R(d_{ik})^{N-1}}{\sum_j \sum_{k(\neq i)} R(d_{jk})^{N-1}} \cdot A_{tot}$.

5.5 References

Andelman, S., and Willig, M.R. 2002. Alternative configurations of conservation reserves for Paraguayan bats: considerations of spatial scale. *Conservation Biology* 16: 1352–1363

Anderson, W.J. 1991. Continuous Time Markov Chains. Springer-Verlag, New York

Berryman, A.A. 1999. Principles of Population Dynamics and their Application. Stanley Thornes Publishers, Cheltenham, UK

Day, J. R., and H. P. Possingham. 1995. A stochastic metapopulation model with variability in patch size and position. Theoretical Population Biology 48: 333-360

Doak, D. F., P. C. Marino, and P. M. Kareiva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. Theoretical Population Biology 41: 315–336

Drechsler, M. 2000. A model-based decision aid for species protection under uncertainty. *Biological Conservation* 94: 23-30

Drechsler, M., and Wissel, C. 1998. Trade-offs between local and regional scale management of metapopulations. *Biological Conservation* 83: 31-41

Drechsler, M., Frank, K., O'Hara, B., Hanski, I., and Wissel, C. 2003. Ranking metapopulation extinction risks for conservation: from pattern to action. *Ecological Applications* 15: 990–998

Etienne, R.S. 2002. Striking the metapopulation balance: Mathematical models and methods meet metapopulation management. PhD Thesis, Wageningen University

Etienne, R.S., Heesterbeek, J.A.P. 2000. On optimal size and number of reserves for metapopulation persistence. *Journal of Theoretical Biology* 203: 33-50

Etienne, R.S., and Heesterbeek, J.A.P. 2001. Rules of thumb for conservation of metapopulations based on a stochastic winking-patch model. *The American Naturalist* 158: 389-407

Frank, K. 2004. Ecologically differentiated rules of thumb for habitat network design – lessons from a formula. *Biodiversity and Conservation* 13: 189–206

Frank, K. 2005. Metapopulation persistence in heterogeneous landscapes: lessons about the effect of stochasticity. *The American Naturalist* 165: 374-388

Frank, K., and C. Wissel. 1998. Spatial aspects of metapopulation survival: from model results to rules of thumb for landscape management. Landscape Ecology 13: 363-379

Frank, K., and Wissel, C. 2002. A formula for the mean lifetime of metapopulations in heterogeneous landscapes. *The American Naturalist* 159: 530-552

Foley, P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. *Conservation Biology* 8: 124-137

Goodman, D. 1987. The demography of chance extinction. In: Soulè, M.E. (ed.) Viable Populations for Conservation. Cambridge University Press, Cambridge. pp. 11–34

Haight, R.G., Cypher, B., Kelly, P.A., Philliips, S., Possingham, H.P., Ralls, K., Starfield, A.M., White, P.J., and Williams, D. 2001. Optimizing habitat protection using demographic models for population viability. *Conservation Biology* 16: 1386–1397

Hanski, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* 63: 151-163

Hanski, I., and Gyllenberg, M. 1993. Two general metapopulation models and the core-satellite hypothesis. *The American Naturalist* 142: 17–41

Hanski, I., and Ovaskainen, O. 2000. The metapopulation capacity of a fragmented landscape. *Nature* 404: 755-758

Heinz, S.K., Conradt, L., Wissel, C., and Frank, K. 2004. Dispersal behaviour in fragmented landscapes: deriving a practical formula for patch accessibility. *Landscape Ecology* (in press)

Heinz, S.K., Wissel, C., and Frank, K. The viability of metapopulations: individual dispersal behaviour matters. *Landscape Ecology* (submitted)

Kirkpatrick, S., Gelatt, C.D. and Vecchi, M.P. 1983. Optimization by simulated annealing. *Science* 220: 671–680

Lawton, J.H. 1999. Are there general laws in ecology?. *Oikos* 84: 177-192

Lindenmayer, D.W., and Possingham, H.P. 1996. Ranking conservation and timber management options for Leadbeater's Possum in southeastern Australia using Population Viability Analysis. *Conservation Biology* 10: 1-18

Metropolis, N.A., Rosenbluth, M., Rosenbluth, A., and Teller, E. 1953. Equation of state calculations by fast computing machines. *Journal of Chemical Physics* 21: 1087–1092

Minc, H. 1988. Nonnegative matrices, Wiley-Interscience Series in Discrete Mathematics and Optimization, John Wiley & Sons, Inc., New York

Murray, B.G. 2000. Universal laws and predictive theory in ecology and evolution. *Oikos* 89: 403-408

Ovaskainen, O. and Hanski, I. 2003. How much does an individual habitat fragment contribute to metapopulation dynamics and persistence? *Theoretical Population Biology* 64: 481-495

Possingham, H.P., Ball, I.R., and Andelman, S. 2000. Mathematical models for reserve design. In: Ferson, S., Burgman, M. (eds.) Quantitative methods for conservation biology. Springer-Verlag, New York.

Stacey, P.B., Johnson, V.A.m and Taper, M.L. 1997. Migration within metapopulations: the impact upon local population dynamics. In: Hanski, I., and Gilpin, M.E. (eds.) Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego, California, pp. 267–291

Stelter, C., Reich, M., Grimm, V., and Wissel, C. 1997. Modelling persistence in dynamic landscapes: lessons from a metapopulation of grasshopper *Bryodema tuberculata*. *Journal of Animal Ecology* 66: 508-518

Turchin, P. 2000. Does population ecology have general laws? *Oikos* 94: 17-26

van Langevelde, F., Schotman, A., Claassen, F., and Sparenburg, G. 2000. Competing land use in the reserve site selection problem. *Landscape Ecology* 15: 243–256

van Langevelde, F., Claassen, F., and Schotman, A. 2002. Two strategies for conservation planning in human-dominated landscapes. *Landscape Urban Planning* 58: 281–295

Verboom, J., Metz, J., and Meelis, E. 1993. Metapopulation models for impact assessment of fragmentation. In: Vos, C.C., Opdam, P. (eds.) Landscape Ecology of a Stressed Environment (IALE Studies in Landscape Ecology 1). Chapman & Hall, London. pp. 172-191

Weaver, J.L., Paquet, P.C., and Ruggiero, L.F. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. *Conservation Biology* 10: 964–976

Wilcove, D.S., McLennan, C.H., and Dobson, A.P. 1986. Habitat fragmentation in the temperate zone. In: Soulé ME (ed.) Conservation Biology. Sinauer, Sunderland. pp. 237–256

Wilson, G.G., and Willis, E.O. 1975. Applied biogeography. In: Cody, M.L., and Diamond, J.M. (eds.) Ecology and Evolution of Communities. Harvard University Press, Cambridge, MA. pp. 523–534.

Wissel, C., Stephan, T., and Zaschke, S.H. 1994. Modelling extinction of small populations. In: Remmert H (ed.) Minimum viable populations (Ecol. Studies 106). Springer-Verlag, Berlin. pp. 67-103

Chapter 6

Unifying deterministic and stochastic metapopulation persistence

This chapter is mainly based on the following publication:

Frank, K. 2005. Metapopulation persistence in heterogeneous landscapes: lessons about the effect of stochasticity. *The American Naturalist* 165: 374-388

As the preceding Chapters (Chapters 3 to 5) demonstrate and as is generally known (e.g. Shaffer 1981; Soulé 1987; Lindenmayer and Possingham 1996; Burgman and Possingham 2000; Coulson *et al.* 2001; Drechsler *et al.* 2003; Westphal *et al.* 2003), mathematical models can considerably contribute to achieving a better understanding of metapopulation persistence and to supporting decision-making. However, some snags still exist: Firstly, there are different model types, which vary in terms of the spatial or temporal structure, or the level of detail (e.g. non-spatial/spatial, deterministic/stochastic, without/with local dynamics) (e.g. Levins 1969; Nisbet and Gurney 1982; Quinn and Hastings 1987; Verboom *et al.* 1991; Wissel and Stöcker 1991; Mangel and Tier 1993; Doak *et al.* 1992 and references therein; Hanski 1994; Day and Possingham 1995; Bascompte and Solé 1996; Drechsler and Wissel 1997; Stelter *et al.* 1997; Frank and Wissel 1998; Johst *et al.* 2002; Ovaskainen 2002; Ovaskainen *et al.* 2002). Secondly, different measures of metapopulation persistence (e.g. Hanski and Ovaskainen 2000; Etienne and Heesterbeek 2001; McCarthy *et al.* 2001, 2003; Frank and Wissel 2002) are considered. This opens the possibility of drawing different conclusions about metapopulation persistence. Hence, a unifying theory of metapopulation persistence is needed. This entails highlighting the consequences of choosing a particular modeling approach, looking for bridges to the other approaches, identifying and explaining common effects and differences, and determining implications for theory and management. This motivated the present study.

In this Chapter, we aim at clarifying some consequences of ignoring and including stochasticity for the analysis of metapopulation persistence. Special emphasis is placed on the effect of the landscape structure in this context. To understand this effect is crucial for both ecological theory and conservation management. Stochasticity is a key factor for metapopulations which are vulnerable to extinction. The source of stochasticity under consideration is the stochasticity in the sequence of the extinction and colonization events. In order to meet this goal, the outcomes of two existing (one deterministic, one stochastic) spatially realistic, Levins-type metapopulation models (Frank and Wissel 1998; Hanski and Ovaskainen 2000) are compared and checked for common effects and differences. One central finding of this study is that, if environmental noise in the local populations is moderate or strong, there are extra effects of the landscape structure on metapopulation persistence in face of stochasticity and an increasing importance of the initial conditions as well. In the result, important absolute and relative conclusions about metapopulation persistence (e.g. persistence status, ranking orders, qualitative trends) are highly sensitive to ignoring and including stochasticity. Evidently, including stochasticity is vital in this case in order to prevent counter-productive conclusions. All the results of the comparative analysis are condensed in “five lessons about the effect of stochasticity”. These lessons are complementary to the “four facts about persistence” by Mangel and Tier (1994). Additionally, some implications of the result for ecological theory (interplay between spatial heterogeneity and stochasticity; combined effects of different sources of stochasticity) and conservation management (rules of thumb; landscape indices as predictors for metapopulation persistence) are discussed. Finally, some general remarks on the potential and demands of the comparative approach taken in this study are drawn.

All the analysis work in this study is based on the recently published formulas for the metapopulation capacity λ_M (Hanski and Ovaskainen 2000), the mean lifetime T_m (Frank and Wissel 2002; see also Chapter 3 in this thesis), and the effective number of patches $\tilde{N}$ (Ovaskainen and Hanski 2004). The study shows how these formulas can serve as powerful tools in comparative persistence analyses to benefit of theory and management.

6.1 Methods

Our aim is to obtain a better understanding of the consequences of ignoring or including stochasticity in connection with the analysis of metapopulation persistence. The source of stochasticity under consideration is the stochasticity in the sequence of extinction and colonization events. In order to meet this goal, we perform a comparative analysis which is based on two existing spatially realistic metapopulations models: one deterministic model (Hanski and Ovaskainen 2000; Ovaskainen and Hanski 2001) and one stochastic model (Frank and Wissel 1998). Each model is a presence-absence continuous time model, i.e. it only takes the occupancy state (occupied, empty) of the patches into account. Extinction and recolonization are the only processes which can cause changes to these states. Each model is Levins-type, i.e. it takes neither rescue-effects (Brown and Kodric-Brown 1977) nor Allee effects (Hanski 1994; Ovaskainen 2002) into account. This assumption, however, is uncritical for the purpose of this study because we are primarily interested in the effect of ignoring and including stochasticity on the model results.

In the following, we briefly describe the two models (state space, parameters). We assemble the definitions and measures of metapopulation persistence used in the two cases and clarify central underlying assumptions. This is done in order to provide a sound basis for the desired comparative analysis and to support understanding of the results.

6.1.1 The deterministic case

6.1.1.1 The model

The deterministic metapopulation model used is the model by Hanski and Ovaskainen (Hanski and Ovaskainen 2000; Ovaskainen and Hanski 2001)

$$\frac{dp_i}{dt} = (\sum_{j(\neq i)} c_{ji} \cdot p_j) \cdot (1 - p_i) - \nu_i \cdot p_i \qquad \text{for all } i \in \{1, ..., N\}, \tag{6.1}$$

where N is the number of patches and $\mathbf{p} = (p_1, ..., p_N)$ the state of the metapopulation given by the probabilities p_i of the individual patches i being occupied. The term c_{ij} denotes the colonization rate, i.e. probability per time of patch i colonizing patch j, and ν_i the local extinction rate, i.e. the probability per time of patch i going extinct. The spatial structure of the habitat network is included by the following standard submodels:

$$\nu_i = e\, A_i{}^{-x} \quad , \quad c_{ij} = y\, A_i{}^{b}\, e^{-\alpha\, d_{ij}} \tag{6.2}$$

(e.g. Wissel *et al.* 1994; Hanski 1994; Foley 1997; see also Chapter 2 in this thesis).

Although the state of the metapopulation $\mathbf{p} = (p_1, ..., p_N)$ is given by probabilities (i.e. p_i), the model is characterized as "deterministic" because it does not take the stochasticity in the sequence of extinction and recolonization processes into account.

If the metapopulation is assumed to be spatially homogeneous, i.e. the model parameters $\nu_i = \nu$ and $c_{ij} = c$ are assumed to be identical for all the patches i, then the spatial model is equivalent to the classical Levins model $\frac{dp}{dt} = c_{tot} \cdot p \cdot (1 - p) - \nu \cdot p$ (Levins 1969) where $c_{tot} = (N - 1) \cdot c$ is the total colonization rate of each patch.

6.1.1.2 Definition and measure of metapopulation persistence

It is known (e.g. Ovaskainen and Hanski 2001) that the solution of system (6.1) always converges to a stable equilibrium $\mathbf{p}^* = (p_1^*, ..., p_N^*)$ that can be determined by repeatedly applying the following iteration rule:

$$p_i = \frac{\sum_{j(\neq i)} c_{ji} \cdot p_j}{\sum_{j(\neq i)} c_{ji} \cdot p_j - \nu_i}. \tag{6.3}$$

This iteration has been found to converge always: either to the extinct state $\mathbf{0} = (0, ..., 0)$ or to a certain non-trivial solution $\mathbf{p}^* > \mathbf{0}$ where at least one component $p_i^* > 0$. Therefore, it makes sense to call a metapopulation to be persistent if it is not extinct in the equilibrium, i.e. $\mathbf{p}^* > \mathbf{0}$. In order to make metapopulations and/or options of metapopulation management comparable, a scalar measure of metapopulation persistence is needed which can be determined from the model parameters (c_{ij}, ν_i).

In the spatially homogenous case, the measure of persistence is evident. Here, the functional structure of the stable equilibrium is explicitly known: $p^* = \max[0, 1 - (c_{tot}/\nu)^{-1}]$. The persistence condition $p^* > 0$ is met if $c_{tot}/\nu > 1$ that is the well-known Levins condition (Levins 1969). Hence, the ratio c_{tot}/ν between the total colonization rate c_{tot} and the local extinction rate ν is an appropriate measure of persistence in this case. It gives the total number of colonizations a local population is able to induce during its life span $1/\nu$. In the spatially heterogeneous case, the situation is more complex because the functional relationship between the stable equilibrium $\mathbf{p}^* = (p_1^*, ..., p_N^*)$ and the model parameters (c_{ij}, ν_i) is not explicitly known. There is only an iteration scheme (6.3) for the determination of $\mathbf{p}^*$. But note that the persistence condition $\mathbf{p}^* > \mathbf{0}$ is equivalent to the loss of stability of the trivial solution $\mathbf{0} = (0, ..., 0)$ of the iteration scheme. By using standard results from calculus, Hanski and Ovaskainen (2000) showed that $\mathbf{0}$ is unstable as long as

$$\lambda_M > 1, \tag{6.4}$$

where λ_M is the leading eigenvalue of the matrix $M = (m_{ij})$ with elements $m_{ij} = c_{ji}/\nu_i$ for $j \neq i$ and $m_{ij} = 0$ else. The authors also showed that λ_M can be approximated by

$$\lambda_M \approx \frac{\sum_{i=1}^{N} srow(i) \cdot scol(i)}{\sum_{k=1}^{N} srow(k)} \tag{6.5}$$

where

$$\begin{aligned} srow(i) &= \sum_j m_{ij} = \sum_{j(\neq i)} c_{ji}/\nu_i = \frac{y}{e} \sum_{j(\neq i)} A_j^b A_i^x e^{-\alpha d_{ji}}, \\ scol(i) &= \sum_j m_{ji} = \sum_{j(\neq i)} c_{ij}/\nu_j = \frac{y}{e} \sum_{j(\neq i)} A_i^b A_j^x e^{-\alpha d_{ij}}. \end{aligned}$$

The term λ_M is a mathematical aggregation of the colonization rates c_{ij} and the local extinction rates ν_j. It is called metapopulation capacity and used as measure of metapopulation persistence in deterministic case (for didactic reasons, we depart from the original notation by Hanski and Ovaskainen (2000) who called $\frac{e}{y} \cdot \lambda_M$ metapopulation capacity).

λ_M can be interpreted as the average colonization ability of the local populations in the case that only one of the patches is occupied. It has been found that, if $\lambda_M > 1$, then

$$1 - {\lambda_M}^{-1} \approx {p_w}^* \tag{6.6}$$

with ${p_w}^* = \sum_i w_i \cdot p_i^*$ being a certain weighted mean of the equilibrium patch occupancy states p_i^*. The weights w_i are determined by the left leading eigenvector of the matrix $B = (b_{ij})$ with elements $b_{ij} = \frac{c_{ji} \cdot p_j^*}{\sum_{k=1}^{N} c_{ki} p_k^*}$. These weights called "patch values" measure the relative long-term contribution of the individual patches to the total colonization events in the metapopulation (Ovaskainen and Hanski 2003). Since the correspondence between ${p_w}^* \approx 1 - {\lambda_M}^{-1}$ and $p^* = 1 - (c_{tot}/\nu)^{-1}$ is obvious, we can conclude that λ_M is the spatial equivalent to the (homogenous) measure of persistence c_{tot}/ν and the threshold condition $\lambda_M > 1$ the spatial equivalent to the (homogeneous) threshold condition $c_{tot}/\nu > 1$.

6.1.2 The stochastic case

6.1.2.1 The model

The stochastic metapopulation model used is the continuous time, finite Markov chain model described in Chapter 2 where the degrees of correlation ρ_{ij} are assumed to be negligible ($\rho_{ij} = 0$). Analogous to the deterministic case, ν_i and c_{kj} denote the (stochastic) extinction and colonization rates, respectively. By using the submodels for ν_i and c_{ij} specified in relation (6.2), the model can be made spatial.

Remember that Markov chain models show a typical dynamic behavior (cf. Chapter 2): If the metapopulation is initially in state $\mathbf{x_0}$ then a certain percentage of the runs indicates a rapid extinction, while the remaining runs indicate a rapid approach to quasi-stationarity. In the result, the survival probability $S_{\mathbf{x_0}}(t)$ of the metapopulation at time t shows the following structure: $S_{\mathbf{x_0}}(t) \approx c_{\mathbf{x_0}} \cdot e^{-t/T_m}$ for larger values of t. The term $c_{\mathbf{x_0}}$ is the probability of the metapopulation successfully approaching quasi-stationarity. It summarizes the effects of the initial state $\mathbf{x_0}$ relevant for persistence. The term $S^*(t) := e^{-t/T_m}$

is the survival probability of the metapopulation after reaching quasi-stationarity. It is determined by the mean lifetime T_m that summarizes the effects of the quasi-stationary phase of the metapopulation dynamics relevant for persistence. T_m is independent of the initial state $\mathbf{x_0}$. Both $c_{\mathbf{x_0}}$ and T_m can be extracted by eigensystem analysis of the transition matrix A underlying the Markov chain model (see Chapter 2).

6.1.2.2 Definition and measure of metapopulation persistence

The relation $S_{\mathbf{x_0}}(t) \approx c_{\mathbf{x_0}} \cdot e^{-t/T_m}$ reveals three serious problems in connection with the definition of metapopulation persistence in the stochastic case: Firstly, the survival probability $S_{\mathbf{x_0}}(t)$ goes to zero with increasing time t. Secondly, $0 < S_{\mathbf{x_0}}(t) < 1$ for each time t. Thus, the question of survival cannot be answered with "yes" or "no" in the absolute sense. Thirdly, this question also depends on the initial state $\mathbf{x_0}$ of the metapopulation. Such an effect is completely missing in the deterministic case. Here, all non-trivial initial states $\mathbf{p_0}$ belong to the range of attraction of the stable equilibrium $\mathbf{p}^*$. This shows that a new definition of metapopulation persistence is needed in the stochastic case.

One option is to fix a certain time horizon t_H and a certain acceptable risk of extinction ε and to call a metapopulation with initial state $\mathbf{x_0}$ to be persistent if it (a) successfully approaches quasi-stationarity with probability

$$c_{\mathbf{x_0}} > 1 - \varepsilon, \tag{6.7}$$

and (b) survives under quasi-stationarity until time t_H with probability $S^*(t_H) > 1 - \varepsilon$. Since $S^*(t_H) = e^{-t_H/T_m}$, the latter condition is equivalent to

$$T_m > \frac{t_H}{-\ln(1-\varepsilon)}. \tag{6.8}$$

This definition of metapopulation persistence can be directly interpreted by conservation biologists who are familiar with dealing with time horizons and risks. This combined $c_{\mathbf{x_0}}$- and $S^*(t_H)$-based approach to persistence is widely used in the context of population viability analysis (e.g. Goel and Richter-Dyn 1974; Nisbet and Gurney 1982; Burgman and Possingham 2000; Possingham *et al.* 2001; Beissinger and McCullough 2002) and is closely related to the concept of "minimum viable population" (e.g. Shaffer 1981; for an overview see Soulé (1987) or Remmert (1994)). Taking 100 or 1000 years as the time horizon t_H and 0.1 or 0.05 as the acceptable risk of extinction ε is quite common in this field. The major advantage of this definition is that it allows the effects of the transient and the quasi-stationary phases of the metapopulation dynamics on the persistence to be separately analyzed. The correspondence between equilibrium and quasi-stationarity ensures a certain comparability between deterministic and stochastic case.

In Chapter 3, we revealed that the mean lifetime T_m can be approximated by

$$T_m \approx T_m^a \left(N, \nu_{agg}, (\tfrac{c_{tot}}{\nu})_{agg}\right) \tag{6.9}$$

where T_m^a is the formula given by equation (3.5) in Chapter 3. The terms ν_{agg} and $(\frac{c_{tot}}{\nu})_{agg}$ are special mathematical aggregations of the model parameters ν_i and c_{ij} (see also relations (3.15; 3.16) in Chapter 3). They can be interpreted as the *effective* local extinction rate and the *effective* colonization ability of the subpopulations. Formula (6.9) was found to be applicable to a wide range of patch configurations in the sense that qualitative and quantitative effects on metapopulation persistence are well reproduced.

For large numbers of patches N, Ovaskainen (2002) developed an alternative approach to deriving effective metapopulation parameters and approximating the mean lifetime T_m. His approach is based on diffusion-approximation (see also Example 4 in Sec. 7.1.2.1 of this thesis). He revealed for a number of examples that $T_m \approx T_m^a(\tilde{N}, \tilde{\nu}, \frac{\tilde{c}_{tot}}{\tilde{\nu}})$, where T_m^a is as above and $\tilde{\nu}$, $\tilde{c}_{tot}$ and $\tilde{N}$ are the effective parameters given by relations (6.14; 6.15; 6.16) in the Appendix. By taking into account that $\tilde{c}_{tot}/\tilde{\nu} = \lambda_M$ (see (6.15)), we obtain

$$T_m \approx T_m^a \left(\tilde{N}, \tilde{\nu}, \lambda_M\right). \tag{6.10}$$

In contrast to formula (6.9), this formula is only partly explicitly expressed in terms of ν_i and c_{ij}. Additionally, macroscopic quantities such as the patch values w_i and the deterministic equilibrium occupancies p_i^* have to be determined before $\tilde{\nu}$, $\tilde{N}$, and, finally, T_m can be calculated (see (6.14; 6.16)). The major advantage of this formula is that its functional structure reveals how the stochastic (T_m) and deterministic (λ_M) measures of metapopulation persistence are related to each other: T_m is nearly a polynomial of λ_M of the order $\tilde{N} - 1$. But note that formula (6.10) is only applicable to metapopulations with a large number of patches N, as is the whole diffusion-based approach.

6.2 Results

This study aims at highlighting some consequences of ignoring or including stochasticity in connection with the analysis of metapopulation persistence. The source of stochasticity considered is the stochasticity in the sequence of the extinction and colonization events.

Special emphasis is placed on the spatial effects on metapopulation persistence and the analysis of their robustness against ignoring or including stochasticity. This especially concerns the relative results (e.g. trends, ranking orders among alternative habitat networks according to their effect on persistence) because they are of particular importance for both theory (understanding the relationship between spatial structure and metapopulation persistence) and conservation management (ranking of management options).

The central question of this study is the following: "When do the two (deterministic/stochastic) approaches to metapopulation persistence described in Section 2 lead to the same conclusions and when to different results?". In order to meet this goal, the results of the deterministic and the stochastic analyses will be compared and checked for common effects and differences. One aspect of particular interest is the role of those elements of the stochastic approach which are missing in the deterministic approach: the time horizon t_H, the acceptable risk of extinction ε, and the initial state of the metapopulation $\mathbf{x_0}$.

6.2.1 A start-up analysis

In order to get an initial impression about the functional relationship between landscape structure and metapopulation persistence and its sensitivity to choosing the deterministic or the stochastic approach for the analysis, we start with a simple experiment. This experiment addresses the following questions: (a) What total amount of habitat is needed in a given habitat network for maintaining metapopulation persistence? (b) What is the effect of the number, the spatial configuration and the relative size of the patches? (c) How robust are the results against ignoring and including stochasticity? (d) What is the role of the initial state $\mathbf{x_0}$, the time horizon t_H and the acceptable risk of extinction ε?

To answer these questions, we consider four hypothetical habitat networks which coincide in the total amount of habitat in the network, A_{tot}, but vary in number and configuration of the patches (see Fig. 1). For didactic reasons, the effect of the relative patch size is analyzed in a hierarchical way. In the first step, we assume that the total amount of habitat A_{tot} is uniformly distributed among the patches. In this case, the area A_i of each patch i is given by $A_i = \frac{1}{N} \cdot A_{tot}$ for all $i \in \{1, ..., N\}$, where N is the number of patches in the relevant habitat network. By applying this rule to all habitat networks considered, we obtain three correspondingly named scenarios ("Net 1", "Net 2", "Net 3a"). In the second step, we abandon the condition of uniform habitat distribution in order to analyze the effect of patch size heterogeneity. Here, we exclusively consider the 9-patch system and assume that the two patches closest to each other (patches 1 and 2 indicated by the arrows in Figure 1C) contain 50% of the total amount of habitat A_{tot}. The other 50% are uniformly distributed among the remaining seven patches. This uneven habitat distribution is modeled as $A_1 = A_2 = \frac{1}{4} \cdot A_{tot}$ and $A_i = \frac{1}{2 \cdot 7} \cdot A_{tot}$ for all $i \in \{3, ..., 9\}$. The corresponding scenario is referred to as "Net 3b".

To obtain insight into the role of the species' ecological attributes, we consider extremely weak ($x = 6$) and moderate environmental noise ($x = 0.8$) in the local populations. After specifying the values for all the other species-ecological parameters (we assume $y = e = 1$, $b = 0.5$, $\alpha = 0.04$), the local extinction rates ν_i and the colonization rates c_{ij} are calculated for each scenario considered by using the submodels (6.2).

Before we can start with the actual analysis, we have to specify the time horizon t_H and the acceptable risk of extinction ε for the stochastic case. We start with $t_H = 100$ years and $\varepsilon = 0.05$. Then the different measures of persistence (one deterministic and two stochastic) are calculated for each scenario. The metapopulation capacity λ_M and the mean lifetime T_m are calculated by using the corresponding approximation formulas (Equation (6.5) for λ_M and Equation (6.9) for T_m). In order assess the relative importance of the initial states $\mathbf{x_0}$ for metapopulation persistence, the percentage $P(c_{\mathbf{x_0}} > 1 - \varepsilon)$ of favorable initial states $\mathbf{x_0}$ meeting the condition $c_{\mathbf{x_0}} > 1 - \varepsilon$ is calculated.

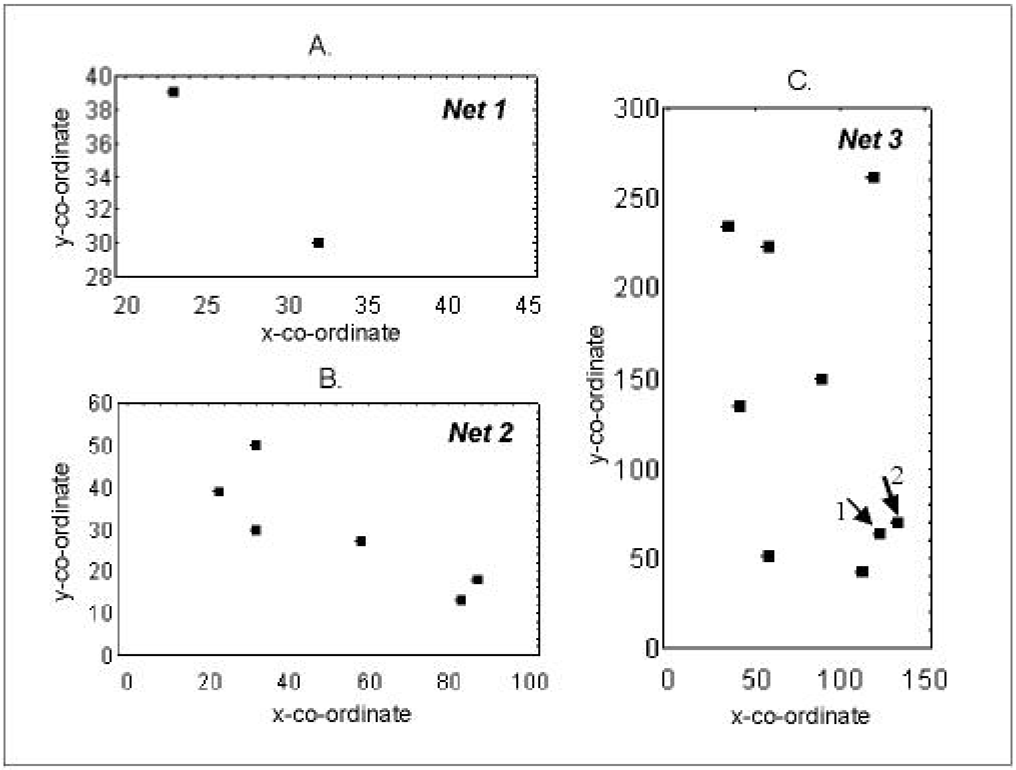

FIGURE 6.1: Three hypothetical habitat networks which are taken as a basis for different scenarios of habitat allocation (three uniform, one uneven). The arrows in Net 3 (C) indicate the two patches which receive above-average amounts of habitat in the uneven scenario (see text).

Figure 6.2 shows the result for the case of weak environmental noise in the local populations. The curves in Figures 6.2A-F reveal a number of common effects in the deterministic and stochastic approaches. Firstly, the arrows in Figures 6.2A and 6.2B indicate that there are critical total amounts of habitat A_{tot}^{crit} above which the deterministic condition $\lambda_M > 1$ (Fig. 6.2A) and the (quasi-stationary) stochastic condition $T_m > \frac{t_H}{-ln(1-\varepsilon)}$ (Fig. 6.2B) for metapopulation persistence are met. In each scenario considered, the stochastic threshold value A_{tot}^{crit} is found to be both robust to variation in the time horizon t_H (Fig. 6.2C) and the acceptable risk of extinction ε (Fig. 6.2D) and close to the corresponding deterministic threshold value A_{tot}^{crit} (cf. Figs. 6.2A and 6.2B). Figures 6.2E-H give insight into the role of the initial state $\mathbf{x_0}$ of the metapopulation. They reveal that, as long as A_{tot} is above the threshold value A_{tot}^{crit} (indicated by the arrow), the percentage $P(c_{\mathbf{x_0}} > 1-\varepsilon)$ of favorable initial states $\mathbf{x_0}$ is ≈ 1. This indicates that almost every initial state $\mathbf{x_0}$ leads to quasi-stationarity such that we have both deterministic and stochastic metapopulation persistence in this range. Only if A_{tot} approaches A_{tot}^{crit}, the value of $P(c_{\mathbf{x_0}} > 1-\varepsilon)$ starts to decline, i.e. there is an increasing percentage of initial states $\mathbf{x_0}$ which fail the condition $c_{\mathbf{x_0}} > 1-\varepsilon$. Here, the question of metapopulation persistence can only be answered in a $\mathbf{x_0}$-dependent way. Note that, in Net 3b (Fig. 6.2H), the decline starts already markedly above A_{tot}^{crit}. This is an effect of spatial heterogeneity (here: patch size heterogeneity in combination with isolation). If the metapopulation is initially in a state where merely small and isolated patches are occupied then there is an increasing risk of extinction before approaching quasi-stationarity. Secondly, the different scenarios considered differ in both the threshold values A_{tot}^{crit} and the λ_M- and T_m-values resulting for a certain fixed value A_{tot}. The ranking orders among the scenarios according to A_{tot}^{crit}, λ_M, and T_m are found to be identical and robust to variation in the time horizon t_H and the acceptable risk of extinction ε (cf. Figs. 6.2A-D). This shows that, in the case of weak environmental noise, important quantitative and qualitative aspects of metapopulation persistence are independent of ignoring or including stochasticity. The deterministic and stochastic approaches have a similar predictive power, as far as absolute and relative conclusions about metapopulation persistence are concerned. However, with increasing spatial heterogeneity in the habitat networks, there is an increasing importance of the initial states.

A totally different picture emerges in the case of moderate environmental noise in the local populations (Figures 6.3A-F). Firstly, as before, there are critical total amounts of habitat A_{tot}^{crit} above which the deterministic condition $\lambda_M > 1$ (Fig. 6.3A) and the (quasi-stationary) stochastic condition $T_m > \frac{t_H}{-ln(1-\varepsilon)}$ (Fig. 6.3B) for metapopulation persistence are met. The deterministic and stochastic threshold values A_{tot}^{crit}, however, now markedly differ in all the scenarios considered. The value A_{tot}^{crit} for Net 1, for instance, is ≈ 2 in the deterministic case (Fig. 6.3A) but ≈ 130 in the stochastic case (Fig. 6.3B). Moreover, there are clear effects of the time horizon t_H and the acceptable risk of extinction ε on the stochastic threshold value A_{tot}^{crit}. Figure 6.3C reveals an increase in A_{tot}^{crit} if the time horizon t_H is enlarged. However, this rise is only significant if the number of patches N is small (Net 1). The effect of the acceptable risk of extinction ε is different.

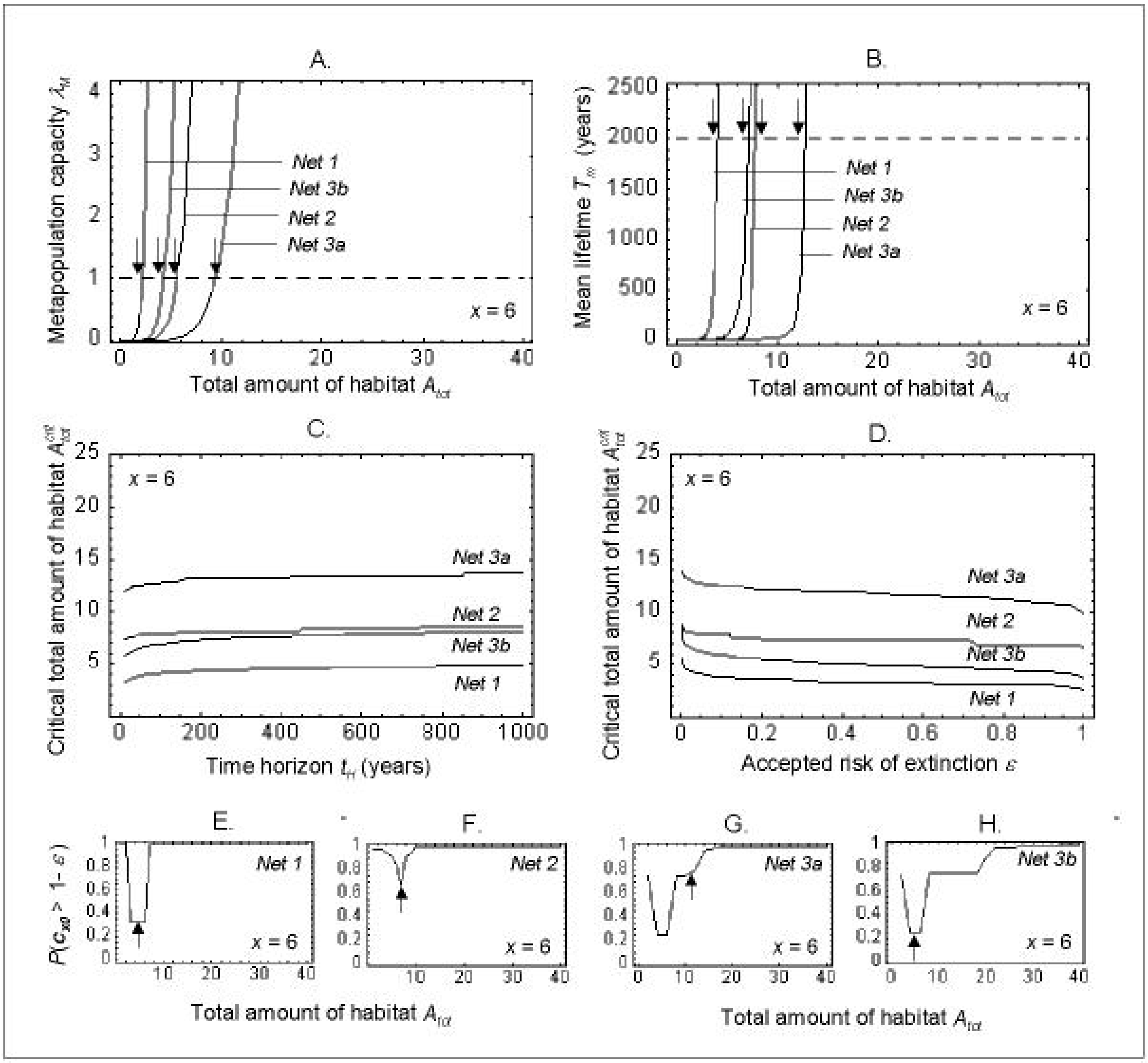

FIGURE 6.2: (A) Metapopulation capacity λ_M and (B) mean lifetime of the metapopulation T_m vs. the total amount of habitat A_{tot} for the three habitat networks given in Figure 6.1, four scenarios of habitat allocation (see text) and weak environmental noise in the local populations ($x = 6$). The dashed lines indicate the threshold values 1 and $\frac{t_H}{-ln(1-\varepsilon)}$ to be exceeded by λ_M and T_m, respectively, where $t_H = 100$ years and $\varepsilon = 0.05$ are assumed. (C and D): Critical total amount of habitat A_{tot}^{crit} resulting from the stochastic model (T_m-analysis) vs. the time horizon t_H with $\varepsilon = 0.05$ (C), and the acceptable risk of extinction ε with $t_H = 100$ years for the three habitat networks considered (D). (E, F, G and H): Percentage $P(c_{\mathbf{x_0}} > 1 - \varepsilon)$ of initial states $\mathbf{x_0}$ meeting the condition for stochastic metapopulation persistence $c_{\mathbf{x_0}} > 1 - \varepsilon$ vs. the total amount of habitat A_{tot} for the four scenarios considered, weak environmental noise ($x = 6$), and $\varepsilon = 0.05$. The arrows indicate the critical A_{tot}^{crit}-values found in Fig. 6.2B.

As is indicated by Figure 6.3D, there is a certain critical value ($\varepsilon \approx 0.1$) above which A_{tot}^{crit} is quite robust to a change in ε, irrespective of the scenario considered. Below this critical value, however, A_{tot}^{crit} is found to be highly sensitive to ε. This sensitivity is especially high if the metapopulation is small (Net 1). Figures 6.3E-H give insight into the role of the initial state $\mathbf{x_0}$ of the metapopulation. In the two 9-patch scenarios (Net 3a and 3b; Figs. 6.3G-H), $P(c_{\mathbf{x_0}} > 1 - \varepsilon)$ is markedly < 1 in the whole range of A_{tot}-values considered. Around 50% of the initial states $\mathbf{x_0}$ is found to be critical. As before, this is an effect of the spatial heterogeneity. The negative effect of patch smallness and isolation is amplified by the stronger environmental noise (smaller x, higher extinction rate $\nu_i = {A_i}^{-x}$).

Another interesting effect can be seen in the 2-patch scenario (Fig. 6.3E). Here, $P(c_{\mathbf{x_0}} > 1 - \varepsilon)$ is ≈ 1 for A_{tot}-values far below A_{tot}^{crit} (see the arrow). In this case, the limiting factor for stochastic metapopulation persistence is primarily the quasi-stationary behavior (T_m) and not the initial state. This also indicates, the two quantities T_m and c_{x_0} actually measure different aspects of stochastic metapopulation persistence. Secondly and even more importantly, the ranking orders among the different scenarios according to the threshold values A_{tot}^{crit}-values markedly differ in the deterministic and stochastic cases. The same is true for the ranking orders according to the λ_M- and T_m-values resulting for a certain fixed value A_{tot}. Both can be seen by comparing the deterministic ranking order ((Net 1, Net 2, Net 3b, Net 3a); Fig. 6.3A) with the stochastic ranking order ((Net 2, Net 3a, Net 3b, Net 1); Fig. 6.3B). Net 1 (2 patches), for instance, is found to be best in the first case but worst in the latter case. Changes in the ranks are obviously not restricted to small metapopulations. As can be seen, Net 3b (9 patches/uneven habitat distribution) is found to be better than Net 3a (9 patches/uniform habitat distribution) in the deterministic case, while the opposite is true in the stochastic case. This indicates that the spatial structure of the habitat networks (number, spatial configuration, relative size of patches) has an extra-effect on metapopulation persistence if stochasticity is included. All these findings reveal that, in the case of moderate environmental noise, several quantitative and qualitative effects on metapopulation persistence are highly sensitive to ignoring or including stochasticity, even if the number of patches N is large.

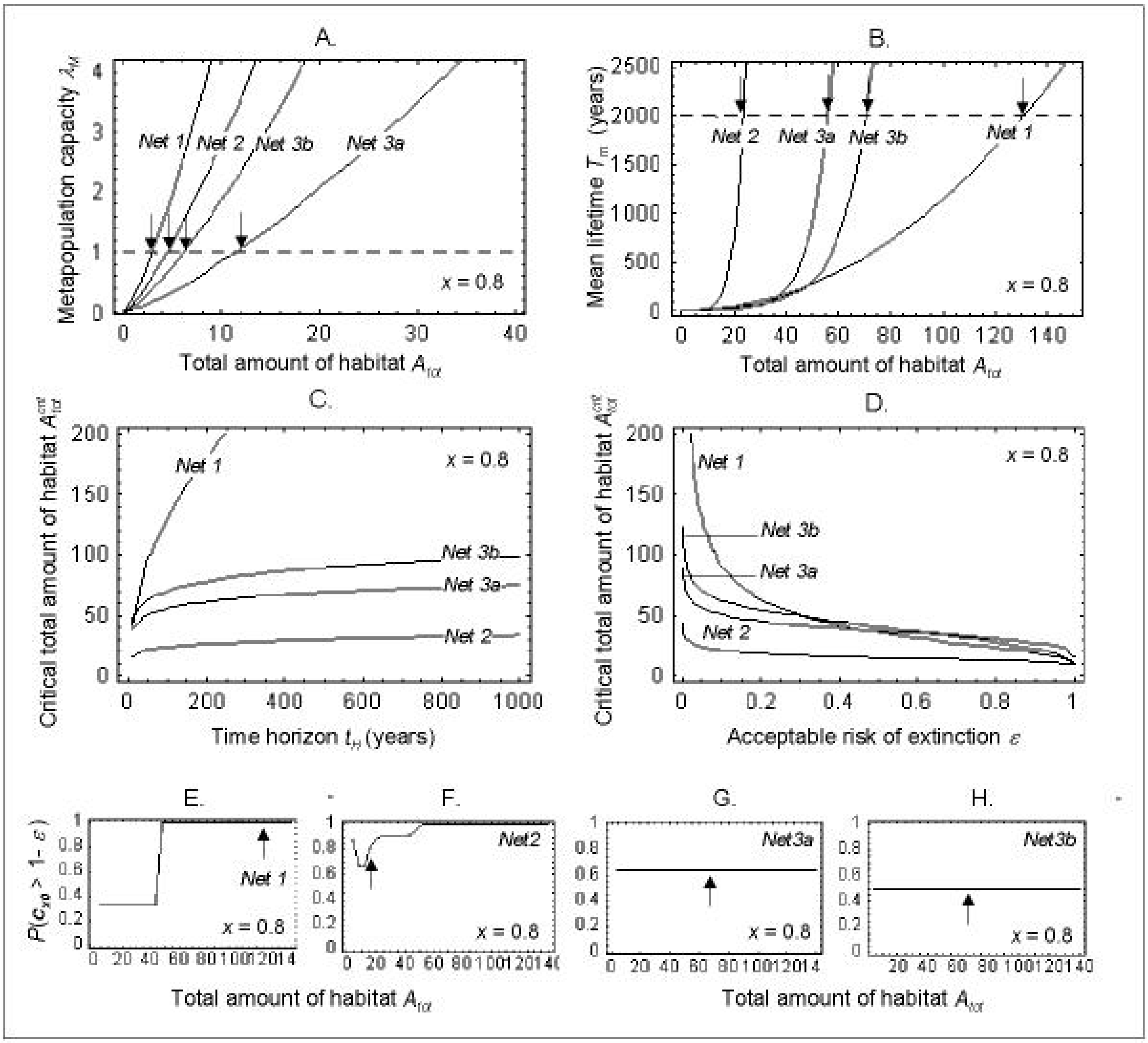

FIGURE 6.3: As Figure 6.2, but with moderate environmental noise ($x = 0.8$).

To summarize, one central result of the start-up experiment is the following finding: Depending on the strength of environmental noise in the local populations, there can be extra effects of the spatial structure of the habitat networks on metapopulation persistence if stochasticity in the sequence of extinction and colonization events is taken into account. Since this finding would have numerous implications for theory and management, we have to clarify whether the effects revealed are just artifacts of the particular habitat networks and/or species' attributes considered or whether they are more generally valid.

6.2.2 A more systematic analysis

In order to obtain a better understanding of the effects revealed (e.g. extra effects of spatial structure under stochasticity, role of the strength of the environmental noise), we continue with a more systematic analysis of the functional structure of the approximation formulas for the two measures of metapopulation persistence used: the metapopulation capacity λ_M (deterministic measure) and the mean lifetime T_m (stochastic measure).

As can be seen, the formula for λ_M (formula (6.5)) can be rewritten as a product

$$\lambda_M \approx \frac{\sum_i (\sum_j \frac{c_{ji}}{\nu_i}) \cdot (\sum_j \frac{c_{ij}}{\nu_j})}{\sum_i \left(\frac{1}{2}(\sum_j \frac{c_{ji}}{\nu_i} + \sum_j \frac{c_{ij}}{\nu_j})\right)^2} \cdot \frac{\sum_i \left(\frac{1}{2}(\sum_j \frac{c_{ji}}{\nu_i} + \sum_j \frac{c_{ij}}{\nu_j})\right)^2}{\sum_i \left(\frac{1}{2}(\sum_j \frac{c_{ji}}{\nu_i} + \sum_j \frac{c_{ij}}{\nu_j})\right)} \tag{6.11}$$

The first factor is always ≤ 1 because $(\sum_j \frac{c_{ji}}{\nu_i}) \cdot (\sum_j \frac{c_{ij}}{\nu_j}) \leq (\frac{1}{2}(\sum_j \frac{c_{ji}}{\nu_i} + \sum_j \frac{c_{ij}}{\nu_j}))^2$ (remember: geometric mean $\leq$ arithmetic mean). It reaches its maximum value 1 if $\sum_j \frac{c_{ji}}{\nu_i} = \sum_j \frac{c_{ij}}{\nu_j}$ for all i, i.e. if the colonization activity *into* patch i is equal to the colonization activity *from* patch i. The second factor is a self-weighted mean of the total colonization activity $\frac{1}{2}(\sum_j \frac{c_{ji}}{\nu_i} + \sum_j \frac{c_{ij}}{\nu_j})$ of the individual patches i. As is typical for self-weighted means, it increases with increasing variance in $\frac{1}{2}(\sum_j \frac{c_{ji}}{\nu_i} + \sum_j \frac{c_{ij}}{\nu_j})$ and becomes maximum if the colonization power is concentrated to a few patches. This shows that spatial heterogeneity is favorable for λ_M and (deterministic) metapopulation persistence (see also Hanski and Ovaskainen 2000). This result corresponds with Adler and Nuernberger (1994), who found that (deterministic) metapopulation persistence benefits from a clumped patch configuration. It also explains why Net 1 (2 patches) is found to be best for λ_M, Net 3a (9 patches/uniform habitat distribution) to be worst and Net 3b (9 patches/uneven habitat distribution) to be better than Net 3a (cf. ranking orders of A_{tot}^{crit} in Figs. 6.2A and 6.3A).

How is the situation for the mean lifetime T_m? To answer this question, we analyze the diffusion-based formula (6.10) for $T_m \approx T_m^a(\tilde{N}, \tilde{\nu}, \lambda_M)$, which indicates that T_m is a polynomial of λ_M of the order $\tilde{N}$-1 and a pre-factor $1/\tilde{\nu}$. This shows that the overall effect of the spatial structure on T_m and so on (stochastic) metapopulation persistence consists of two components: the deterministic effect (summarized in λ_M) and additional effects (summarized in $\tilde{\nu}$ and $\tilde{N}$). But as the calculation in the Appendix (relations (6.17) to (6.20)) reveals, the effective number of patches $\tilde{N}$ (relation (6.16)) can be algebraically transformed such that the effect of spatial structure can simply be read off. We obtain

$$\tilde{N} \;\approx\; \frac{\displaystyle\sum_{i=1}^{N} \frac{w_i \cdot {\nu_i}^{-1}}{\sum_k w_k \cdot {\nu_k}^{-1}} \cdot \nu_i\, p_i^*}{\displaystyle\sum_{i=1}^{N} \frac{{w_i}^2}{\sum_k {w_k}^2} \cdot \nu_i\, p_i^*} \cdot \frac{1}{1 + \frac{\operatorname{Var} W}{(\operatorname{E} W)^2}} \cdot N. \tag{6.12}$$

This shows that $\tilde{N}$ is approximated by a product of three factors: the actual number of patches N, a ratio between two specially weighted means of $\nu_i\, p_i^*$, and a term $\frac{1}{1+\frac{\operatorname{Var} W}{(\operatorname{E} W)^2}}$ determined by the relative variance $\frac{\operatorname{Var} W}{(\operatorname{E} W)^2}$ of the patch values w_i. In the case of spatial homogeneity ($\nu_i = \nu$, $c_{ij} = c$), we find that $\tilde{N} = N$, i.e. the effective and actual numbers of patches coincide (note that all the p_i^*s and w_is are constant and $\operatorname{Var} W = 0$ in this case; see also Ovaskainen and Hanski (2004)). Increasing variance in the patch values w_i, however, resulting from rising heterogeneity in the spatial configuration reduces the effective number of patches $\tilde{N}$. This functional relationship between spatial heterogeneity and the effective number of patches $\tilde{N}$ is a formal reflection of the fact that an uneven distribution of the colonization activity causes an above-average risk of fatal sequences of extinction events if some of the “main colonization players” go extinct. Note that the decreasing effect of spatial heterogeneity on $\tilde{N}$ is opposite to the increasing effect on λ_M. Evidently, there is a trade-off between λ_M and $\tilde{N}$ in the face of stochasticity. Which part dominates the threshold condition $T_m^a(\tilde{N}, \tilde{\nu}, \lambda_M) > \frac{t_H}{-\ln(1-\varepsilon)}$ depends on the pre-factor $1/\tilde{\nu}$, i.e. the effective local lifetime of the local populations. This quantity determines the contribution of local persistence to metapopulation persistence within the time horizon t_H, the demand on the collective colonization success and, therefore, the relative importance of the effective number of patches $\tilde{N}$. This especially explains the effect of the environmental noise in the local populations x revealed. As long as this noise is weak (x large), there is long-term local persistence ($1/\tilde{\nu}$ large), prompting the low importance of $\tilde{N}$ and the dominance of λ_M. As a result, all the effects of the spatial structure on metapopulation persistence coincide in the deterministic and the stochastic cases. They are summarized in λ_M. Increasing environmental noise in the local populations (decreasing x and $1/\tilde{\nu}$), however, increases the importance of $\tilde{N}$ and, hence, the need to take the trade-off between

λ_M and $\tilde{N}$ into account. This trade-off effect explains in particular the ranking orders in Figure 6.3B: it reveals why Net 2 (6 patches) is found to be best (benefit for λ_M and $\tilde{N}$), Net 1 (2 patches) to be worst ($\tilde{N}$ too small), and Net 3a to be better than Net 3b ($\tilde{N}$ is higher for a uniform than for an uneven distribution of habitat).

To summarize, the structural analysis of the approximation formulas for the metapopulation capacity λ_M and the mean lifetime T_m revealed that spatial heterogeneity has a positive effect on λ_M and a trade-off effect on T_m. In the result, differences in the response of λ_M and T_m to changes in the landscape structure have to be expected which are the more likely the less persistent the local populations are. This phenomenon is generally valid and independent of the details of the extinction and colonization processes.

6.3 Discussion

This study addressed an important aspect of the analysis of metapopulation persistence. Its major aim was to highlight consequences of ignoring and including stochasticity in the sequence of the extinction and colonization events ("extinction-colonization stochasticity") for the derivation of (absolute and relative) conclusions about metapopulation persistence. To meet this goal, we performed a comparative analysis of one deterministic and one stochastic approach to metapopulation persistence. In the following, we take the results of this study as a basis and derive a list of both those effects which are common in the two approaches and those which are really "extra" if stochasticity is included and which are not covered by the deterministic approach. We discuss important implications of these findings for ecological theory and conservation management. We finish with some methodological remarks on the comparative approach followed in this study.

6.3.1 Five lessons about the effects of stochasticity

In the following, we want to condense the results of this study into a few "lessons" about the effects of stochasticity in connection with the analysis of metapopulation persistence:

Lesson 1: In both approaches, metapopulation persistence is determined by the mean of threshold conditions. But there are two major differences. Firstly, two conditions are needed for characterizing metapopulation persistence in the stochastic approach: one on the initial state ($c_{\mathbf{x_0}} > 1-\varepsilon$) and one on the quasi-stationary behaviour ($T_m > \frac{t_H}{-\ln(1-\varepsilon)}$) of the metapopulation. In the deterministic approach, a single condition on the equilibrium behaviour ($\lambda_M > 1$) suffices; a $\mathbf{x_0}$-dependent component is missing because convergence to the equilibrium is certain for each non-trivial initial state $\mathbf{x_0}$. Secondly, the threshold values $1-\varepsilon$ and $\frac{t_H}{-\ln(1-\varepsilon)}$ to be exceeded in face of stochasticity are not constant as in the deterministic case but dependent on the subjective perspective of the decision-maker, i.e. the time-horizon t_H and the acceptable risk of extinction ε.

Lesson 2: The measure of deterministic metapopulation persistence, $\lambda_M \approx (1-p_w^*)^{-1}$ (remember (6.6)), indicates that it suffices to analyze an appropriately weighted mean of the equilibrium occupancy pattern, p_w^*, to draw correct conclusion about deterministic metapopulation persistence. The two measures of stochastic metapopulation persistence, $c_{\mathbf{x_0}}$ and $T_m \approx T_m^a(\tilde{\nu}, \tilde{N}, \lambda_M)$ (see (6.10)), reveal that this is not enough in face of stochasticity. Here, the effective local lifetime of the local populations, $1/\tilde{\nu}$, the effective number of patches, $\tilde{N}$, and the initial state, $\mathbf{x_0}$, have additionally to be taken into account.

Lesson 3: In the case of moderate or strong environmental noise in the local populations ($x < 1.5$), there is an extra effect of spatial structure (number of patches, spatial heterogeneity) on metapopulation persistence in face of stochasticity. In the deterministic case, *heterogeneity* in the colonization abilities and concentration to *few* strong local populations is advantageous for metapopulation persistence. In the stochastic case, however, there is a need to support both a high colonization ability (λ_M) and a medium effective number of patches ($\tilde{N}$) in order to avoid fatal sequences of extinction events. As a result of the latter condition, a *medium* number of patches and *homogeneity* in the colonization abilities of the local populations become decisive. This difference between the deterministic and stochastic effects of spatial structure on metapopulation persistence has a serious consequence: if alternative patch configurations are assessed and compared regarding their effect on λ_M (deterministic persistence) and T_m (stochastic persistence), the resulting ranking orders can differ. This means that ignoring or including extinction-colonization stochasticity can lead to different relative results and to different qualitative trends.

Lesson 4: The subjective perspective of the decision-maker (the time horizon t_H, the acceptable risk of extinction ε) has a noticeable effect if the effective number of patches (spatial heterogeneity!) is small (≤ 5) or if $\varepsilon < 0.1$. But note that this is the range of ε-values which is usually used in the context of population viability analysis and which is relevant for conservation management (risk aversion).

Lesson 5: Including stochasticity in the sequence of extinction and colonization events is indispensable for avoiding counter-productive conclusions about metapopulation persistence if the environmental noise in the local populations is moderate or strong. The same is true if the habitat network is highly spatially heterogeneous and the colonization ability is concentrated to a few strong local populations. In this case, the question of metapopulation persistence strongly depends on the initial state $\mathbf{x_0}$.

The lessons presented are complementary to the four facts about persistence by Mangel and Tier (1994). While the the "four facts" address important local effects on the persistence of single populations, our "five lessons" focus on the persistence of metapopulations with special respect to the effects of spatial structure in interplay with stochasticity, to the role of the subjective aspects of the assessment (the time horizon t_H, the acceptable risk of extinction ε), and to the initial state $\mathbf{x_0}$ of the metapopulation.

None of the lessons supports a "precise" determination of extinction thresholds in any concrete case study. But this goal cannot be met anyway because the models under consideration are rather generic and, hence, too rough to allow predictions for concrete metapopulations. Moreover, all the models are of the Levins type and ignore important effects such as Allee and rescue effects. First and foremost, the lessons provide a better understanding of some fundamental consequences of ignoring or including stochasticity for the analysis of metapopulation persistent. They reveal that ignoring or including stochasticity may have quantitative and qualitative effects, even if the (actual) number of patches N is large. They reveal important conditions under which including stochasticity is vital to prevent counter-productive conclusions concerning metapopulation persistence.

6.3.2 Implications for ecological theory

The results of this study (especially Lesson 3) also contribute to the debate on the role of spatial structure for ecological processes (e.g. Doak *et al.* 1992; Durrett and Levin 1994; Adler and Nuernberger 1994; Day and Possingham 1995; Bascompte and Solé 1996, 1998; With and King 1999; Fahrig 2001, 2002). They especially provide new insights into the effect of the landscape structure on stochastic metapopulation persistence. But they also have relevance for other fields of ecology such as epidemiology because there is a strong analogy between epidemiological and metapopulation models (e.g. Anderson and May 1991; Nee 1994; Grenfell and Harwood 1997; Amarasekare and Possingham 2001).

6.3.2.1 Extra effects of the landscape structure in face of stochasticity

We revealed that an increasing heterogeneity in the colonization abilities of the local populations always has a positive effect on λ_M (deterministic persistence) but a trade-off effect on T_m (stochastic persistence). This structural difference in the responses of λ_M and T_m gave rise to the following conclusion: There is an extra effect of the landscape structure on metapopulation persistence in face of stochasticity the relative importance of which is the higher the less persistent the local populations are. This is certainly the most important finding of this study (see also Lesson 3). This extra effect is caused by the interplay between the spatial heterogeneity and the extinction-colonization stochasticity. This interplay primarily influences the risk of suffering from fatal sequences of extinction events. An (inverse) measure of this risk is the effective number of patches $\tilde{N}$ (see (6.12)). We showed that an increasing heterogeneity in the colonization abilities of the local populations always causes a decrease in $\tilde{N}$ and, hence, an increasing risk of fatal sequences of extinction events. This counteracts the positive effect on λ_M and explains the trade-off effect on T_m. Note that all these results are direct benefits of the comparison between T_m and λ_M. They could not have been derived with analyzing only one of them alone.

6.3.2.2 Interplay between environmental noise and extinction-colonization stochasticity

Lesson 3 reveals an additional interesting point that is worth being discussed in more detail. It indicates that the strength of the environmental noise in the local populations determines the extent to which the extinction-colonization stochasticity can influence the functional relationship between landscape structure and metapopulation persistence, i.e. can alter trends and ranking orders. This shows that important (quantitative and even qualitative) persistence effects of one source of stochasticity can markedly depend on the strength of another source of stochasticity at another (here: lower) organizational level. In such situations, correct conclusions about persistence can only be drawn if the interplay between the different sources of stochasticity at the different levels is taken into account. Further research is needed to obtain a better understanding of such combined stochastic effects and their consequences for stochastic (meta-)population persistence.

6.3.3 Implications for conservation management

Conservation management strongly depends on information about trends and ranking orders among alternative scenarios (e.g. management options, landscape configurations) according to their effect on (meta-)population persistence. As is known, models can be very useful tools for providing this information (e.g. Bascompte and Solé 1996; Lindenmayer and Possingham 1996; Frank and Wissel 1998; Burgman and Possingham 2000; Coulson *et al.* 2001; Drechsler *et al.* 2003; Westphal *et al.* 2003; Frank 2004). The present study, however, reveals a serious problem in connection with metapopulation management. It indicates that trends and ranking orders are not robust to choosing a deterministic or a stochastic model for the persistence analysis. This is especially the case if the environmental noise in the local populations is moderate or strong (see also Lessons 3 and 5). Here, the use of stochastic models is vital for preventing counter-productive conclusions about metapopulation persistence. But now another problem comes to light. All model-based tools of decision-support which aim at ranking landscape scenarios have to be assessed regarding whether they are based on a deterministic or on a stochastic model.

6.3.3.1 Check the assumptions of rules of thumb

Rules of thumb for landscape management are common and widely discussed. They condense important qualitative effects of the landscape structure on (meta-)population persistence in a verbal way (e.g. Wilson and Willis 1975; Wilcove *et al.* 1986; Adler and Nuernberger 1994; Day and Possingham 1995; Frank and Wissel 1998; Etienne and Heesterbeek 2000, 2001; Frank 1998, 2004). To clarify the assumptions and ranges of applicability of every rule of thumb is highly relevant for landscape management, as the following example demonstrates. At a first glance, the two rules of thumb "Clumping and patch size variability are favorable for metapopulation persistence" (Adler and Nuernberger 1994) and "Patch size homogeneity is favorable for metapopulation persistence if colonization is strong enough" (Day and Possingham 1995) seem to be contradicting. A more careful check of the two rules, however, revealed that the first rule is based on a deterministic model. Hence, it is only applicable as long as the environmental noise in the local populations is weak. The second rule is based on a stochastic model with moderate environmental noise in the local populations ($x = 1$). This shows that the two rules simply have complementary ranges of applicability.

6.3.3.2 Ecologically scaled landscape indices as predictors of persistence

In the recent landscape ecological literature, there is a debate on the development of ecologically scaled landscape indices and their use as predictors for landscape effects on population dynamics (e.g. Schumaker 1996; Frank and Wissel 1998, 2002; Wiegand *et al.* 1999; Hanski and Ovaskainen 2000; Vos *et al.* 2001). Such indices take important characteristics of both the landscape structure and the species' ecology into account.

In connection with metapopulations, there is a discussion on whether the fraction of occupied patches (or a related quantity such as p_w^*) is a useful predictor for metapopulation persistence. Regarding deterministic persistence, the question is fully and positively answered because Ovaskainen and Hanski (2001) proved the correspondence between p_w^* and $1 - {\lambda_M}^{-1}$ and showed that p_w^* is a much better predictor than the total amount of habitat A_{tot}, or the number of patches N. Regarding stochastic persistence, however, the discussion is ongoing. Vos *et al.* (2001) performed a model analysis and concluded that p_w^* is also a useful predictor for stochastic metapopulation persistence. They especially proposed that the threshold condition $p_w^* > (0.4 \text{ to } 0.6)$ indicates stochastic persistence.

The findings of the recent study indicate that these statements are not valid in general and have to be differentiated. To see this, take into account that $S^*(100) = e^{-100/T_m}$, $T_m \approx T_m^a(\tilde{\nu}, \tilde{N}, \lambda_M)$ (see (6.10)), and $\lambda_M \approx (1 - p_w{}^*)^{-1}$ (remember (6.6)). Therefore,

$$S^*(100) \approx e^{-100/T_m^a(\tilde{\nu}, \tilde{N}, (1-p_w^*)^{-1})}. \tag{6.13}$$

This relation gives the relationship between $S^*(100)$ and p_w^*. Figures 6.4A-B show some $S^*(100)$ vs. p_w^* curves for different values of $\tilde{N}$ and $\tilde{\nu}$. Although the curves markedly differ, they corroborate that $p_w^* < 0.4$ indicates non-persistence, irrespective of $\tilde{N}$ and $\tilde{\nu}$.But we also see that the threshold condition $p_w^* > (0.4 \text{ to } 0.6)$ does not yet guarantee stochastic metapopulation persistence in general, as was proposed by Vos *et al.*. This condition is only sufficient as long as the effective number of patches $\tilde{N}$ is relatively large, namely ≥ 15 for medium-term local persistence ($\tilde{\nu} = 0.1$; Fig. 6.4A) and ≥ 20 for short-term local persistence ($\tilde{\nu} = 0.5$; Fig. 6.4B). It does not work for smaller effective numbers of patches $\tilde{N}$ which are particularly relevant in connection with conservation questions (note that $\tilde{N}$ can be small even if the actual number of patches N is large because $\tilde{N}$ decreases with increasing spatial heterogeneity). Vos *et al.* considered metapopulations with seven to fifty patches, i.e. large systems. Even more critical is the fact that p_w^* does not always allow ranking orders in the $S^*(100)$-values to be correctly reflected. p_w^* only works as long as the environmental noise in the local populations is low, but fails if the noise becomes moderate or strong (cf. Figs. 6.4C-D). To be fair, Vos *et al.* could not find this effect because they did not vary the strength of environmental noise in their study.

All these findings corroborate what we already formulated in Lesson 2: the fraction of occupied patches p_w^* alone is unable to correctly predict metapopulation persistence in face of stochasticity. This is especially the case if the environmental noise in the local populations is moderate or the effective number of patches is small. Here, the only appropriate predictor is the mean lifetime T_m. But note that the aggregation-based approximation formula $T_m^a(\nu_{agg}, N, (\frac{c_{tot}}{\nu})_{agg})$ (see (6.9)) applied to appropriate spatial submodels for ν_i

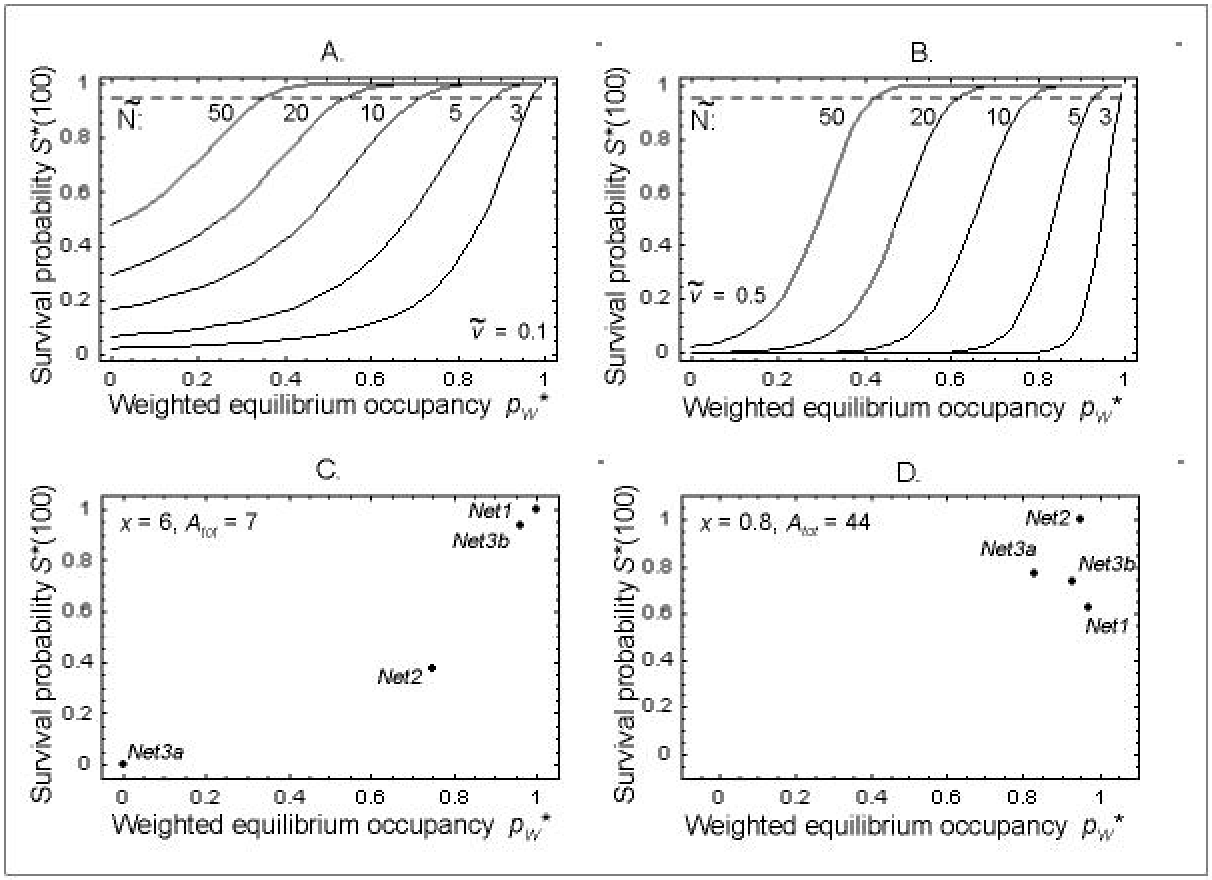

FIGURE 6.4: (A and B) Survival probability $S^*(100)$ for a quasi-stationary metapopulation after 100 years (calculated with equation (6.13)) versus the weighted mean equilibrium occupancy p_w^* (see text) for different effective numbers of patches $\tilde{N}$ and effective local extinction rates $\tilde{\nu}$ of 0.1 (A) and of 0.5 (B). The dashed line denotes the 0.95-threshold. (C-D) $S^*(100) = e^{-100/T_m}$ vs. $p_w^* \approx (1 - \lambda_M)^{-1}$ calculated from the T_m- and λ_M-values for the four scenarios considered in Figures 6.2A-B and 6.3A-B with ($A_{tot} = 7$, $x = 6$) (C) and ($A_{tot} = 44$, $x = 0.8$) (D), respectively.

and c_{ij} (e.g. (6.2)) gives an ecologically scaled landscape index which meets all the requirement: It is expressed in terms of spatial as well as species-ecological attributes and allows correct conclusions about stochastic metapopulation persistence to be drawn.

6.3.4 Some general remarks on the approach presented

The main idea of the approach taken in this study was to compare the outcome of two (one deterministic, one stochastic) metapopulation models and to seek common effects, differences, and possible reasons. This supported a better understanding of important quantitative and qualitative effects of stochasticity on metapopulation persistence with implications for theory building and conservation management. But the study was only successful because a number of favorable conditions were met.

6.3.4.1 Complementary but comparable model structures

Ignoring and including a certain factor and comparing the resulting outcomes is a common way of analyzing its relative importance. This shows that each of the two models used was indispensable for obtaining a comprehensive understanding of the effects of stochasticity in the context of metapopulation persistence. But note that the comparison was markedly facilitated by the fact that the two models have comparable model structures, i.e. they work on the same levels of detail (finite, presence-absence, Levins-type models) and refer to the same model parameters (c_{ij}, ν_i, N).

6.3.4.2 Approximation formulas for the measures of persistence

The present study especially benefited from the fact that approximation formulas for the (deterministic and stochastic) measures of metapopulation persistence and their ingredients (the effective parameters; see also Section 7.1.2) were available: one formula for the metapopulation capacity λ_M and even two formulas for the mean lifetime T_m working on different levels of resolution (microscopic, macroscopic) with complementary advantages.

As the λ_M-formula (equation (6.5)), the aggregation-based T_m-formula (equation (6.9)) is completely expressed in terms of the main model parameters (N, c_{ij}, ν_i). This means that, once the local extinction rates ν_i and colonization rates c_{ij} are known, these two formulas allow the values for λ_M and T_m to be directly calculated. In this way, they enable a decision-maker to perform comparative analyses of metapopulation persistence and to check the robustness of the results to ignoring or including stochasticity.

The diffusion-based T_m-formula (equation (6.10)) has the advantage that it clarifies the functional relationship between T_m and λ_M, and reveals that all the extra effects of the interplay between spatial heterogeneity and stochasticity are summarized in the effective local extinction rate $\tilde{\nu}$ and the effective number of patches $\tilde{N}$.

The two (aggregation-based and diffusion-based) approximation formulas for the mean lifetime T_m were derived in totally different ways. Even so, they reflect important qualitative effects on metapopulation persistence in exactly the same way and give rise to the same ecological conclusions. The two formulas thus qualitatively validate each other.

The main achievement of the formulas, however, became apparent when the effects of spatial heterogeneity were analyzed (see Sec. 6.3.2). As we saw, it proved possible by algebraic transformation to express λ_M and $\tilde{N}$ in terms of variances of certain patch-specific quantities (i.e. of the total colonization activities $\frac{srow(i)+scol(i)}{2}$ in (6.11) and of patch values w_i in (6.12)) which can be directly related to spatial heterogeneity. This allowed general conclusions to be drawn on the effect of spatial heterogeneity on metapopulation persistence. These conclusions are independent of the details of the functional dependence of ν_i and c_{ij} on landscape structure and species' ecology. But note that they depend on the assumption that neither rescue nor Allee effects are involved because they are based on Levins-type models. Comparing the resulting deterministic and stochastic "principles" enables a comprehensive understanding of the main effects of stochasticity on a rather general level. The advantage of combining numeric and algebraic analyses was already demonstrated in Chapter 5, where ecologically differentiated rules of thumb for habitat allocation and a Principle of Optimality for metapopulation persistence were derived on the basis of the (aggregation-based) formula for T_m. All these arguments show the potential of the approximation formulas for λ_M (Hanski and Ovaskainen 2000), T_m (Frank and Wissel 2002), and $\tilde{N}$ (Ovaskainen 2002; Ovaskainen and Hanski 2004).

6.4 Appendix

The effective parameters $\tilde{N}, \tilde{\nu}, \tilde{c}_{tot}$ derived by Ovaskainen (2002)

For larger values of N, Ovaskainen (2002) showed that $T_m \approx T_m^a(\tilde{N}, \tilde{\nu}, \frac{\tilde{c}_{tot}}{\tilde{\nu}})$ for a large number of examples. The effective parameters $\tilde{N}, \tilde{\nu}$, and $\tilde{c}_{tot}$ are given by

$$\begin{aligned}
\tilde{\nu} &= (\sum_{i=1}^{N} w_i \cdot {\nu_i}^{-1})^{-1}, && (6.14)\\
\tilde{c}_{tot} &= \tilde{\nu} \cdot \lambda_M, && (6.15)\\
\tilde{N} &= \frac{\tilde{c}_{tot} \cdot p_w^*(1-p_w^*) + \tilde{\nu} \cdot p_w^*}{\sum_{i=1}^{N} {w_i}^2 \cdot [(\sum_{j(\neq i)} c_{ji} \cdot p_j^*)(1-p_i^*) + \nu_i \cdot p_i^*]} && (6.16)
\end{aligned}$$

with $p_w^* = \sum_{i=1}^{N} w_i \cdot p_i^*$ (see also Ovaskainen and Hanski (2004)). The p_i^*s are the deterministic equilibrium occupancies and the weights w_i the patch values discussed in Section 6.2.

Algebraic transformation of the effective number of patches $\tilde{N}$

Below, the formula for the effective number of patches $\tilde{N}$ by Ovaskainen and Hanski (2004) (see also equation (6.16) in the present study) will be algebraically transformed such that the effect of spatial heterogeneity can be directly analyzed. Starting point of the calculation is the fact that $(p_1^*, ..., p_N^*)$ used in formula (6.16) is the equilibrium occupancy state of the spatial Levins-model (6.1). Therefore, $(\sum_{j(\neq i)} c_{ji} \cdot p_j^*)(1-p_i^*) = \nu_i \cdot p_i^*$ for all i. Furthermore, it is evident that p_w^* approximates the equilibrium occupancy state of the related classical Levins model $\frac{dp}{dt} = \tilde{c}_{tot} \cdot p(1-p) - \tilde{\nu} \cdot p$ because $p_w^* = \sum_i w_i \cdot p_i^* \approx 1 - {\lambda_M}^{-1} = 1 - (\tilde{c}_{tot}/\tilde{\nu})^{-1}$, as can be concluded from both relation (6.6) (see also Ovaskainen and Hanski (2001; 2003)) and the definition of the effective colonization rate $\tilde{c}_{tot} = \lambda_M \cdot \tilde{\nu}$ (see (6.15)). Consequently, $\tilde{c}_{tot} \cdot p_w^*(1-p_w^*) \approx \tilde{\nu} \cdot p_w^*$. This results in the following simplification of the original formula for $\tilde{N}$:

$$\tilde{N} = \frac{\tilde{c}_{tot} \cdot p_w^*(1-p_w^*) + \tilde{\nu}\, p_w^*}{\sum_i {w_i}^2 \cdot \Big[(\sum_{j(\neq i)} c_{ji} \cdot p_j^*)(1-p_i^*) + \nu_i\, p_i^*\Big]} \approx \frac{2 \cdot \tilde{\nu}\, p_w^*}{2 \cdot \sum_i {w_i}^2 \cdot \nu_i\, p_i^*}. \qquad (6.17)$$

Inserting the definitions of $\tilde{\nu} = (\sum_i w_i \cdot {\nu_i}^{-1})^{-1}$ (see (6.14)) and $p_w^* = \sum_k w_k \cdot p_k^*$ in (6.17) leads to:

$$
\begin{aligned}
\tilde{N} \approx \frac{\tilde{\nu}\, p_w^*}{\sum_i {w_i}^2 \cdot \nu_i\, p_i^*} &= \frac{1}{\sum_i w_i \cdot {\nu_i}^{-1}} \cdot \frac{\sum_k w_k \cdot p_k^*}{\sum_i ({w_i}^2 \cdot \nu_i\, p_i^*)} \\
&= \frac{1}{\sum_i w_i \cdot {\nu_i}^{-1}} \cdot \frac{\sum_k (w_k \cdot {\nu_k}^{-1}) \cdot (\nu_k\, p_k^*)}{\sum_i ({w_i}^2 \cdot \nu_i\, p_i^*)} \\
&= \frac{\sum_k \frac{w_k \cdot {\nu_k}^{-1}}{\sum_i w_i \cdot {\nu_i}^{-1}} \cdot \nu_k\, p_k^*}{\sum_i {w_i}^2 \cdot \nu_i\, p_i^*} \\
&= \frac{\sum_k \frac{w_k \cdot {\nu_k}^{-1}}{\sum_i w_i \cdot {\nu_i}^{-1}} \cdot \nu_k\, p_k^*}{\sum_i \frac{{w_i}^2}{\sum_k {w_k}^2} \cdot \nu_i\, p_i^*} \cdot \frac{1}{\sum_k {w_k}^2}. \qquad (6.18)
\end{aligned}
$$

This shows that $\tilde{N}$ is the product of a ratio of two specially weighted means of $\nu_i\, p_i^*$ and the inverse of $\sum_k {w_k}^2$. Note that the w_ks are weights such that $\sum_k w_k = 1$. Therefore,

$$
\begin{aligned}
\frac{1}{\sum_k {w_k}^2} = \frac{(\sum_k w_k)^2}{\sum_k {w_k}^2} &= \frac{(\frac{1}{N}\sum_k w_k)^2}{\frac{1}{N}\sum_k {w_k}^2} \cdot N \\
&= \frac{(\frac{1}{N}\sum_k w_k)^2}{(\frac{1}{N}\sum_k w_k)^2 + \left(\frac{1}{N}\sum_k {w_k}^2 - (\frac{1}{N}\sum_k w_k)^2\right)} \cdot N \\
&= \frac{(\mathrm{E}\, W)^2}{(\mathrm{E}\, W)^2 + \mathrm{Var}\, W} \cdot N = \frac{1}{1 + \frac{\mathrm{Var}\, W}{(\mathrm{E}\, W)^2}} \cdot N, \qquad (6.19)
\end{aligned}
$$

where $\mathrm{E}\, W$ and $\mathrm{Var}\, W$ denote the expected value and the variance of the w_ks. By inserting the last term (6.19) in relation (6.18), we obtain

$$
\tilde{N} \approx \frac{\displaystyle\sum_{k=1}^{N} \frac{w_k \cdot {\nu_k}^{-1}}{\sum_i w_i \cdot {\nu_i}^{-1}} \cdot \nu_k\, p_k^*}{\displaystyle\sum_{i=1}^{N} \frac{{w_i}^2}{\sum_k {w_k}^2} \cdot \nu_i\, p_i^*} \cdot \frac{1}{1 + \frac{\mathrm{Var}\, W}{(\mathrm{E}\, W)^2}} \cdot N. \qquad (6.20)
$$

6.5 References

Adler, F. R., and B. Nuernberger. 1994. Persistence in patchy irregular landscapes. Theoretical Population Biology 45: 41–75

Amarasekare, P., and H.P. Possingham. 2001. Patch dynamics and metapopulation theory: the case of successional species. Journal of Theoretical Biology 209: 333-334

Anderson, R., and R. May. 1991. Infectious diseases of humans. Oxford University Press

Bascompte, J. and R.V. Solé. 1996. Habitat fragmentation and extinction thresholds in spatially implicit models. Journal of Animal Ecology 65: 465–473

Bascompte, J., and R. V. Solé, eds. 1998. Modeling Spatiotemporal Dynamics in Ecology. Springer-Verlag, Berlin

Beissinger, S. R., and D. R. McCullough (eds.). 2002. Population Viability Analysis. University of Chicago Press, Chicago

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58: 445–449

Burgman, M., and H. P. Possingham. 2000. Population viability analysis for conservation: the good, the bad and the undescribed. In A.G. Young, and G. M. Clarke (eds.). Genetics, Demography and Viability of Fragmented Populations, Cambridge University Press, London, 97-112

Coulson, T., Mace, G. M, Hudson, E., and H.P. Possingham. 2001. The use and abuse of population viability analysis. Trends in Ecology and Evolution, 16: 219-221

Darroch, J.N., E. Senata. 1965. On quasi-stationary distributions of absorbing discrete-time finite Markov chains. Journal of Applied Probability 2: 88-100

Day, J. R., and H. P. Possingham. 1995. A stochastic metapopulation model with variability in patch size and position. Theoretical Population Biology 48: 333-360

Doak, D.F., P.C. Marino, and P.M. Kareiva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersing success: Implications for conservation. Theoretical Population Biology 41: 315

Durrett, R., and S. Levin. 1994. Stochastic spatial models: a user's guide to ecological applications. Philosophical Transactions of the Royal Society London B 343: 329–350

Drechsler, M., and C. Wissel. 1997. Separability of local and regional dynamics in metapopulations. Theoretical Population Biology 51: 9–21

Drechsler, M., Frank, K., Hanski, I., O'Hara, B., and, C. Wissel. 2003. Ranking metapopulation extinction risk: from patterns in data to conservation management decisions. Ecological Applications 15: 990–998

Etienne, R. S., and J. A. P. Heesterbeek. 2000. On optimal size and number of reserves for metapopulation persistence. Journal of Theoretical Biology 203: 33-50

Etienne, R.S., and J.A.P. Heesterbeek 2001. Rules of thumb for conservation of metapopulations based on a stochastic winking model. The American Naturalist 158: 389-407

Fahrig, L. 2001. How much habitat is enough?. Biological Conservation 100: 65–74

Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. Ecological Applications 12: 346–353

Foley, P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. Conservation Biology 8: 124-137

Frank, K. 1998. Optimizing a network of patchy habitats: from model results to rules of thumb for landscape management. In: Munro, N.W.P. and Willison, J.H.M. (Hrsg.) Linking Protected Areas with Working Landscapes Conserving, SAMPAA, Wolfville, Nova Scotia, 59-72

Frank, K. 2004. Ecologically differentiated rules of thumb for habitat network design - lessons from a formula. Biodiversity and Conservation 13: 189–206

Frank, K., and C. Wissel. 1998. Spatial aspects of metapopulation survival: from model results to rules of thumb for landscape management. Landscape Ecology 13: 363-379

Frank, K., and C. Wissel. 2002. A formula for the mean lifetime of metapopulations in heterogeneous landscapes. The American Naturalist 159: 530 - 552

Gillespie, D. 1977. Master equations for random walk with arbitrary pausing time distributions. Physical Letters 64A: 22

Goel, N. S., and N. Richter-Dyn. 1974. Stochastic Models in Biology. Academic Press, New York

Grenfell, B., and J. Harwood. 1997. (Meta)population dynamics in infectious diseases. Trends in Evolution and Ecology 12: 395–399

Grimm, V., and Wissel, C. 2004. The intrinsic mean time to extinction: a unifying approach to analyzing persistence and viability of populations. Oikos 105: 501-511

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63: 151–163

Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. Nature 404: 755-758

Johst, K., R. Brandl, and S. Eber. 2002. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. Oikos 98: 263-270

Keilson, J. 1979. Markov Chain Models - Rarity and Exponentiality (Applied Mathematical Sciences 28). Springer Verlag, New York

Lindenmayer, D.W. and H.P. Possingham. 1996. Ranking conservation and timber management options for Leadbeater's Possum in southeastern Australia using Population Viability Analysis. Conservation Biology 10:235-251.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15: 237–240

Mangel, M., and C. Tier. 1993. Dynamics of metapopulations with demographic stochasticity and environmental catastrophes. Theoretical Population Biology 44: 1–31

Mangel, M., and C. Tier. 1994. Four facts every conservation biologist should know about persistence. Ecology 73: 607–614

McCarthy, M.A., Possingham, H.P., Day, J.R., and A.J. Tyre. 2001. Testing the accuracy of population viability analysis. Conservation Biology 15: 1030–1038

McCarthy, M.A., Andelman, S., and Possingham, H.P. (2003). Reliability of relative predictions in population viability analysis. Conservation Biology 17: 982-989

Nee, S. 1994. How populations persist. Nature 367: 123–124

Nisbet, R. M., and W. S. C. Gurney. 1982. Modelling fluctuating populations. John Wiley & Sons, New York

Ovaskainen, 0. 2002. The effective size of a metapopulation living in a heterogeneous patch network. The American Naturalist 160: 612–628

Ovaskainen, O., and Hanski, I. 2001. Spatially structured metapopulation models: global and local assessment of metapopulation capacity. Theoretical Population Biology 60: 281–304

Ovaskainen, O. and Hanski, I. 2003. How much does an individual habitat fragment contribute to metapopulation dynamics and persistence? Theoretical Population Biology 64: 481-495

Ovaskainen, O. and Hanski, I. 2004. Metapopulation dynamics in highly fragmented landscapes. in I. Hanski, and O. Gaggiotti (eds.) Ecology, Genetics, and Evolution in Metapopulations, Academic Press, pp. 73-103

Ovaskainen, O., K. Sato, J. Bascompte, and I. Hanski. 2002. Metapopulation models for extinction threshold in spatially correlated landscapes. Journal Theoretical Biology 215: 95–108

Pollett, P.K. 1997. Limiting conditional distributions for metapopulation models. in A.D. McDonald, and L. McAleer (eds.) Proc. Int. Congr. on Modeling and Simulation, Vol. 2, Modeling and Simulation Society of Australia, Hobart, Australia, 807–812

Possingham, H. P., D. B. Lindenmayer, and M. A. McCarthy. 2001. Population Viability Analysis. Encyclopedia of Biodiversity 4: 831-843

Quinn, J.F., and A. Hastings. 1987. Extinction in subdivided habitats. Conservation Biology 1: 198–208

Remmert, H. (ed.) 1994. Minimum Viable Populations. (Ecol. Studies 106), Springer Verlag, Berlin

Schumaker, N.H. 1996. Using landscape indices to predict habitat-connectivity. Ecology. 77: 1210–1225

Shaffer, M.L. 1981. Minimum viable population sizes for species conservation. Pacific Conservation Biology 1: 39-45

Soulé, M. E. (ed.) 1987. Viable Populations for Conservation. Cambridge University Press, Cambridge

Stelter, C., M. Reich, V. Grimm, and C. Wissel. 1997. Modelling persistence in dynamic landscapes: lessons from a metapopulation of grasshopper *Bryodema tuberculata*. Journal of Animal Ecology 66: 508–518

Verboom, J., K. Lankester, and J.A.J. Metz. 1991. Linking local and regional dynamics in stochastic metapopulation models. Biol. J. Linnean Society 42: 39–55

Vos, C.C., Verboom, J., Opdam, P., and C. Ter Braak. 2001. Toward ecologically scaled landscape indices. The American Naturalist 157: 24–41

Westphal, M.I., Pickett, M., Wayne, M. G., and H. Possingham. 2003 The use of stochastic dynamic programming in optimal landscape reconstruction for metapopulations. Ecological Applications 13: 545–555

Wiegand, T., J. Naves, T. Stephan, and A. Fernandez. 1998. Assessing the risk of extinction for brown bear (*Ursus arctos*) in the Cordillera Cordillera Cantabrica, Spain. Ecological Monographs 68: 539–570

Wiegand, Th., Moloney, K.A., Naves, J., and F. Knauer. 1999. Finding the missing link between landscape structure and population dynamics: a spatially explicit approach. The American Naturalist: 154: 605–627

Wilcove, D.S., McLennan, C.H., and A.P. Dobson. 1986. Habitat-fragmentation in the temperate zone. in: M.E. Soulé (ed.) Conservation Biology. Sinauer, Sunderland, 237–256

Wilson G.G. and E.O. Willis. 1975. Applied biogeography. in: M.L. Cody and J.M. Diamond (eds.) Ecology and Evolution of Communities. Harvard University Press, Cambridge, MA523–534

Wissel, C., and S. Stöcker. 1991. Extinction of populations by random influences Theoretical Population Biology 39: 315-328

Wissel, C., Th. Stephan, and S.-H. Zaschke. 1994. Modelling extinction of small populations. In: Remmert, H. (ed.) Minimum Viable Populations. (Ecol. Studies 106), Springer Verlag, Berlin, 67–103

With, K. A., and A. W. King. 1999. Extinction thresholds for species in fractal landscapes. Conservation Biology 13: 314–326

Wright, S. 1938. Size of population and breeding structure in relation to evolution. Science 87: 430–431

Part III

Beyond metapopulation persistence

In Part II of this thesis (Chapters 3 to 6), we addressed several aspects of metapopulation persistence and contributed to both theory building and management support in this field.

Theory building.– We contributed to the further development of the concept of "metapopulation persistence". We provided new insights into the role of the interplay between spatial heterogeneity, stochasticity and species' ecology in this context. We contributed to the unification of deterministic and stochastic metapopulation persistence.

Management support.– We were able to clarify important principle aspects of metapopulation management (e.g. minimum conditions for long-term metapopulation persistence; optimum habitat allocation; choice of an appropriate approach for the landscape analysis). Additionally, we were able to develop model-based tools for decision-support such as rules of thumb and a formula for the mean lifetime T_m of metapopulations that can be interpreted as a special landscape index. Both have been found to be powerful.

The type of questions addressed is not only relevant in the context of metapopulations but in other fields of ecological research and conservational landscape management as well. For the work in Part II, however, special forms of model building and model analysis were needed. Hence, it is useful to reflect the work in Part II and to make the methodological experience gained usable for other applications. This motivated Part III of this thesis.

Aim of Part III

In the following, we depart from the analysis of metapopulation persistence. We shift the focus of attention to (A) methodological aspects of using models for theory building and management support in the context of applied ecology, (B) implications of the attainable model results for various interdisciplinary aspects of environmental research and conservational landscape management, and (C) some prospects for further research.

A. Methodological development work.– This work is done in three different contexts. In Chapter 7, we address methodological aspects of model building and model analysis that become relevant if generalization and unification are the aim. Generalization and unification are central for both theory building and management support. Special emphasis is placed on mastering two particular challenges which arise in the context of organismic ecology: (a) bridging between specific case studies and general concepts, and (b) managing biocomplexity. A systematic methodology to master these challenges is missing so far. We review both the modeling work performed in this thesis and the literature and assemble approaches and methods that prove to be appropriate. In Chapter 8, we develop a systematic approach and a rough protocol for the derivation of ecologically differentiated rules of thumb. In Chapter 9, we do the same for (meta)population dynamical landscape indices. In both cases, approach and protocol are missing so far. In all cases, the presented approaches, protocols and methods are supplemented with a number of illustrative examples. This is done in order to give a living impression about how one can work with each method in a concrete case and what one can gain from it. The examples are taken from both this thesis and the literature. This helps to understand the results of this thesis as part of a larger system and clarifies the interrelationships.

B. Implications.– All the methods presented in Part III have a range of applicability that goes beyond the analysis and management of (single species) metapopulation persistence, i.e. the original focus of this thesis. This concerns the support of generalization and unification as well as the derivation of ecologically differentiated rules of thumb and (meta)population dynamical landscape indices. Fields of extension are for example:

Original focus (Parts I & II)	*Fields of extension (Part III)*
Single species	Classes of species
Metapopulations	Spatially structured populations
Measures of persistence T_m, λ_M	Other (meta)population dynamical quantities Q
Patchy landscapes	Complex landscapes
Changes in landscape structure	Other critical impacts on biodiversity

As we have seen in Part II of this thesis, ecologically differentiated rules of thumb and (meta)population dynamical landscape indices are powerful tools for predicting and analyzing in (theoretical and applied) population ecology. In Part III (Chapters 8 and 9), we go a step further and demonstrate that both additionally provide *bridges to various fields of environmental research* beyond population ecology. We show that they have serious implications for community ecology and biodiversity research in general, but also for landscape ecology and various interdisciplinary aspects of conservational landscape management: landscape planning, the development of economic instruments including conceptual aspects of ecological economics, integrated assessment. Moreover, we discuss parallels to road ecology and ecotoxicology where the approach of classifying species according to their sensitivity to certain critical impacts is used as well (see also Fig. III.1).

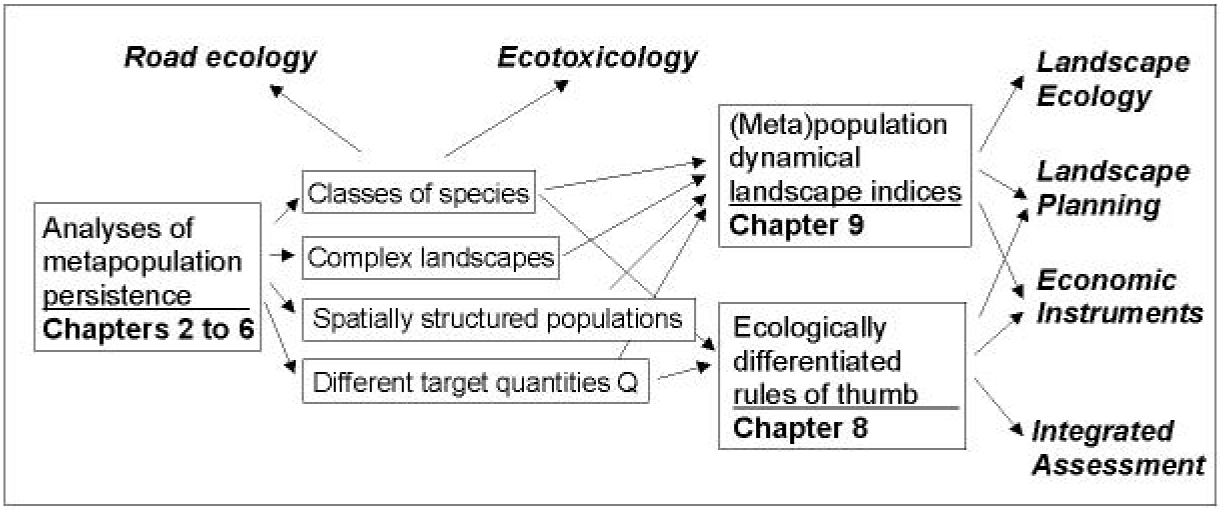

FIGURE III.1: Implications of this thesis for different fields of environmental research

C. Prospects.– The third objective of Part III is the indication of prospects for further research. This is done in the context of the individual chapters. The prospects concern ecological research, interdisciplinary aspects of conservation management and modeling.

Character of Chapters 7, 8, and 9

The character of Part III markedly differs from that of Part II. In Part II, all chapters (Chapters 3 to 6) address a particular ecological question and present a particular way to answer it. This includes the development of the methods needed, a comprehensive analysis of the problem addressed and a sound discussion of the results. In contrast to this, all chapters in Part III (Chapters 7 to 9) basically consist of *review and synthesis* work supplemented with new insights attained from this work. Three different sources of knowledge serve as basis for the review and synthesis work: (a) the results of this thesis, (b) results from co-operation projects with colleagues, and (c) of course, literature. The individual chapters, however, do *not* claim to be comprehensive. They primarily aim at broaching the implications of this thesis, the connections to other fields of recent ecological and environmental research, and some possibilities for further development. But they also aim at giving a rough impression about the scientific profile of the candidate.

As was already mentioned, numerous examples presented in Chapters 7 to 9 come from co-operation projects with colleagues such as PhD or other projects supervised by the candidate (*) or "normal" research co-operations (†). For the original work, see:

† Frank, K. & Ring, I. (1999) Model-based criteria for the effectiveness of conservation strategies: an evaluation of incentive programs in Saxony, Germany. In: Ring, I., Klauer, B., Wätzold, F. und Mansson, B. (Hrsg.) Ecological Economics, Physica Berlin, 91-106

* Heinz, S.K., Conradt, L., Wissel, C. & Frank, K. (2005) Dispersal behaviour in fragmented landscapes: A practical formula for patch accessibility. *Landscape Ecology* (in press)

* Heinz, S.K., Wissel, C. & Frank, K. On the viability of metapopulations: individual dispersal behaviour matters. *Landscape Ecology* (submitted)

* Pe'er, G., Saltz, D. & Frank, K. (2005) Virtual corridors: the concept and its implications for conservation management. *Conservation Biology* (in press)

* Pe'er, G., Heinz, S.K. & Frank, K. (2005) Connectivity in heterogeneous landscapes: analyzing the effect of topography. *Landscape Ecology* (in press)

* Tluk von Toschanowitz, K. (2002) Der Einfluß von Straßennetz und Verkehrsfluss auf die Überlebensfähigkeit von territorialen Wildtierpopulationen: Eine Modellanalyse. Diplomarbeit Universität Osnabrück

† Westphal, M.I. & Frank, K. On rules of thumb for the design of metapopulations (manuscript)

Chapters 7 to 9 are not yet published so far.

Chapter 7

Towards generalization and unification under biocomplexity

One of the great challenges in the context of theory building and management support are the generalization and unification of the profusion of (existing and ongoing) studies.

In the field of *ecological research and theory building*, the need of generalization and unification is obvious for two reasons: Firstly, there is an increasing number and diversity of specific case studies. Case studies have a clear strength because they bring new ecological phenomena to light and allow complex ecological interactions to be analyzed in concrete situations. But in view of their ability to contribute to a comprehensive mechanistic understanding, it is especially important and worthwhile to manage their diversity and to bring the different lines together. One way is to perform comparative analyses and to search for common effects, differences and the reasons behind. This certainly stimulates theory building and, hence, increases the chance of making the scientific knowledge obtained from the case studies "more sustainable". Secondly, there is a problem with the theory building itself: it evolved a life of its own with the result of diverse approaches with own terminology, methods and hypotheses. For an example, remember the two different approaches to metapopulation persistence: the deterministic and the stochastic approach. As an intrinsic by-product of this "own life", there is an increasing risk that theory moves away from reality. This shows that both a unification of the different approaches and a closer linkage between general concepts and specific case studies are required.

As far as *conservation management* is concerned, generalization is even more urgent. There are numerous powerful case studies where extensive field work is combined with extensive model analyses. In the result, detailed recommendations for conservation management (e.g. in the realm of species' protection plans) can be derived which are specifically geared to the given species in the given landscape. This is certainly the best case, but is not attainable in general. It is impossible to start a new empirical study and/or a new specific model analysis for each new situation. One way to overcome this drawback is to take the existing case studies as a basis and to scan them for typical patterns or general principles determining persistence in a wide range of situations. Searching for general principles is especially useful if knowledge about (a) relative trends (e.g. ranking orders among management scenarios according to their effect on persistence), (b) minimum or optimum conditions for persistence, or (c) the effects of uncertainty is needed as a basis for decision-making. Principles give at least a rough orientation for setting management priorities or estimating the effectiveness of a planned management measure.

All these arguments indicate the need of a framework for analysis and synthesis *across different levels of abstraction*: from case studies via models to concepts (for theory and management, respectively) and vice versa (see the scheme in Figure 7.1). Such an iterative approach bridges the gap between general concepts and case studies and enables their advantages to be combined: On the one side, concept-based case studies have the advantage of being intrinsically comparable to each other. On the other side, the close link to the case studies ensures that the conceptual work is anchored in reality. The applicability of concepts and hypotheses to concrete situations can be tested and conceptual deficits can be derived. Moreover, case studies can induce new hypotheses and even new scientific questions. Models represent the decisive bridge between case studies and concepts.

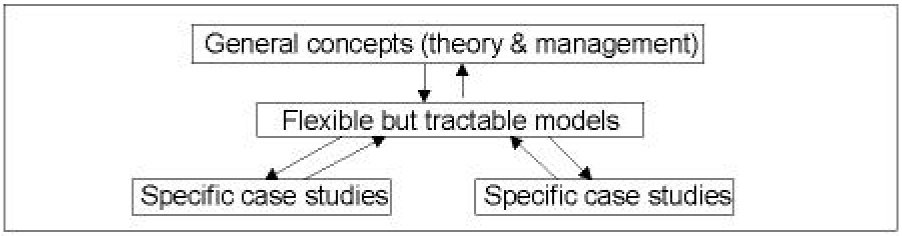

FIGURE 7.1: Analysis across different levels of abstraction: case studies, models, concepts

To bridge between case studies and concepts requires an appropriate model and an appropriate model analysis. The models, for instance, have to be flexible enough to be applicable to a wide range of situations, but also tractable to allow general results to be derived.

If we are interested in generalization/unification in the context of organismic ecology, an additional challenge comes into play: *biocomplexity* as part of ecological realism. Three different sources of biocomplexity can be distinguished (see the scheme in Fig. 7.2). Firstly, processes on various organismic levels (e.g. individuals, populations, metapopulations, species communities) can interact and influence the dynamics of the ecological system considered. Secondly, on each particular organismic level, a multitude of factors and processes can be relevant. Thirdly, each process can be influenced by biological variability (e.g. spatial heterogeneity, temporal variation, individual variability).

In the context of the metapopulation analyses presented in this thesis (Chapters 3 to 6), we were confronted with both the need to bridge between case studies and concepts and the need to manage the full range of biocomplexity. Even so, we were able to derive some general findings on the concept of "metapopulation persistence" and to derive model-based tools for decision-support in conservational landscape management (e.g. rules of thumb, landscape indices for predicting metapopulation persistence). This led to the idea to reflect the way how models were built and analyzed in this thesis and to document the methodological experience gained. In the following, we assemble approaches and methods of model building and model analysis which have proved to be appropriate for the support of generalization and unification. We supplement all the approaches and methods presented with examples from both this thesis and the literature. We finalize with some general conclusions and some prospects for further research.

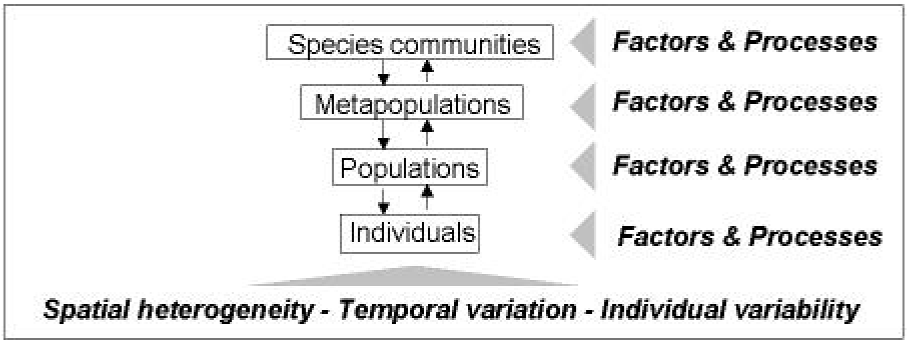

FIGURE 7.2: Three sources of biocomplexity

7.1 Appropriate model building

There are powerful approaches to integrate ecological realism in models. One of them is the development of rule-based models. Prominent examples of these models are individual-based and spatially realistic simulation models (DeAngelis and Gross 1992; Pulliam *et al.* 1992; Dunning *et al.* 1995; Grimm 1999; Wiegand *et al.* 1999; for an overview over the merits of individual-based models, see Grimm and Railsback 2005). These models allow the entire life history and the behavior of the individuals to be described, but also their interactions between each other and their response to the landscape structure. They primarily focus on the lowest organizational level (i.e. individuals), but allow processes from other levels to be included as well, if the need arises. One major advantage of these models is that the can be closely adapted to any particular case study considered. This advantage, however, becomes a disadvantage if generalization and unification are the aim. Firstly, the high level of detail makes these models hardly applicable to other situations. Secondly, these models usually contain a huge number of parameters that counteracts the tractability. Hence, alternatives are needed to the “all-in-one” modeling strategy.

In the following, we demonstrate that the mentioned methodological drawbacks can be partly overcome. We present strategies for managing two sources of biocomplexity: (a) the multitude of organismic levels involved, and (b) the effect of biological variability. Both strategies have been used for model building in preparation of the analyses of metapopulation persistence presented in Part II of this thesis (Chapters 2 to 6).

7.1.1 Managing the multitude of organismic levels: hierarchical model building

As was already mentioned, factors and processes on different organismic levels can influence the dynamics of ecological systems and so the dynamical aspects of particular interest. This multi-level structure, however, also shows a way of how to deal with this source of biocomplexity. One possibility is to follow a hierarchical modeling approach. This means that, in a first step, merely the dynamics on the *highest organismic level* are described by the mean of an appropriate *main model*. In the second step, all the relevant effects of *lower organismic levels* are integrated by the mean of appropriate *submodels*.

7.1.1.1 Generic main models

The heart of any hierarchical model system is a *generic* main model. Generic models merely consider the most essential factors and ignore details. In a multi-level situation such as the recently discussed one, this means the following. The main model has to focus on the highest organismic level that is relevant for the question to be answered. It has to take into account factors, processes, and interactions that are essential on this level.

Example:
In this thesis, we followed a hierarchical approach to model the dynamics of metapopulations. The main model merely considered the occupancy states of the patches but ignored all the details within the patches (e.g. state of the local population, state of the individuals). It merely described the processes that are essential for metapopulations: extinction and colonization. This was done by stochastic rates $\{\nu_i, c_{ij}\}$ (see Chapter 2).

7.1.1.2 Cascades of submodels

All the relevant effects from lower organismic levels can be integrated by using submodels for the main model parameters. Different types of submodels can be used: fully mechanistic (mathematical or simulation) models but also simple input-output rules. To specify the local extinction rates, ν_i, for instance, any stochastic population model can be applied which allows the mean lifetime T_m (and so the reciprocal extinction rate $\nu = 1/T_m$) to be calculated. In this thesis, a well-known input-output relation $\nu_i = A_i^{-x}$ was used. In any case, the submodels ought to be kept as simple as possible. If the need arises, further details can be included by using submodels for submodel parameters. In this way, whole cascades of models - each working on a particular level of detail - can be generated.

Example:
In this thesis, we were working with submodels on two levels of detail. Remember the submodel for the colonization rate $c_{ij} = E_i \cdot a_{ij}$ that expressed c_{ij} in terms of the number of emigrants E_i and the patch accessibility a_{ij}. Additionally, a variety of alternative

submodels (e.g. $a_{ij} = e^{-\alpha \cdot d_{ij}}$, $a_{ij} = \frac{R(d_{ij})^{N-1}}{\sum_k R(d_{ik})^{N-1}} \cdot R(d_{ij})$ with $R(d) = 1 - e^{-a \cdot e^{-b \cdot d}}$) was used to specify the patch accessibility a_{ij} in terms of the landscape structure (d_{ik}) and species' ecological attributes (α or $\{a, b\}$) and according to the movement type.

Modular systems resulting from a hierarchical modeling approach (generic main model, cascades of submodels) are very flexible: the main models can be applied to a wide range of situations and geared to each particular case by choosing appropriate submodels with appropriate parameter values. Moreover, the level of detail of the resulting models can be adapted to the question to be answered and to the empirical data available.

7.1.1.3 Comparison between hierarchical and other modular model systems

Modular model systems are quite common, especially in connection with integrative modeling. But often, these systems are structured in such a way that the modules correspond to the individual processes involved. In the result, the overall dynamics can only be analyzed if all the relevant modules are coupled with each other, that causes complexity again. One major advantage of the hierarchically structured modular system presented is that the generic main model already includes all information about the main processes and interactions between them. In this case, to analyze merely the main model is already sufficient for obtaining at least a rough understanding of the overall dynamics (e.g. relative importance of the individual main processes). By subsequently including submodels, knowledge about the effects of details on lower organismic levels or of biological variability (e.g. spatial heterogeneity, individual variability) can be added subsequently.

7.1.1.4 Range and limitations of applicability of the hierarchical approach

At a first glance, the described hierarchical approach of managing the multitude of organismic levels looks ad hoc. The decisive question is whether including details by submodels leads to the same results as including all the details from the very beginning.

Example:

For the context of metapopulations, the question of the applicability of the hierarchical approach is fully answered (Drechsler and Wissel 1997). The approach is applicable if the local populations show the following dynamical behaviour: they either rapidly go extinct or they rapidly reach quasi-stationarity before extinction. In the consequence, the transition probabilities $P_{nk}(t)$ describing their dynamics can be approximated as follows:

$$P_{nk}(t) \approx h_n \cdot c_k \cdot e^{-\nu \cdot t} \quad \text{for } t \text{ large enough.} \tag{7.1}$$

Hence, the local dynamics are completely characterized by three quantities: the probabilities c_k of reaching quasi-stationarity from a certain state k, the probabilities h_n of being in state n under quasi-stationarity, and the rate of extinction ν under quasi-stationarity (see also Wissel and Stöcker 1991). All these quantities are related to quasi-stationarity of the local populations (Keilson 1979; Pollett 1995, 1997). This justifies to interpret patches as "empty" and "occupied by a quasi-stationary population" and to describe the dynamics of the overall metapopulation as changes in the occupancy states of the patches.

This shows that *explicitly* modeling details of the local dynamics and *implicitly* incorporating their effects by using (h_n), (c_k), ν, and relation (7.1) are equivalent to each other in this case. This is meant in the sense that they effectively lead to the same dynamics $P_{nk}(t)$, the same behavior regarding colonization and extinction, and so the same dynamics of the overall metapopulation. Local and metapopulation processes can be separated from each other without any loss of information, provided (h_n), (c_k), and ν are used as interface. There are standard methods for extracting these quantities from the local details which are based on eigensystem analysis in the case of Markov chain models (Pollett 1995) or on a special numerical protocol for simulation models (Grimm and Wissel 2004).

Drechsler and Wissel (1997) also showed that "rapid transition to extinction or quasi-stationarity" occur in almost all cases, provided (a) the birth rates sufficiently exceed the death rates, (b) the environmental noise in the local populations is not too strong, and (c) the individual exchange between the local populations is not too strong as well. The role of the first two conditions is obvious: both aim at rapidly passing the range of critically small numbers of individuals. The functioning of the third condition is more complex. An increasing individual exchange results in increasing immigration rates with increasing sensitivity to the number of currently occupied patches. Hence, the local dynamics are increasingly affected by the regional dynamics (occurrence of a feedback!) with the consequence that the process of approaching quasi-stationarity is slowed down. All these arguments clarify the *limitations* of applicability of the hierarchical approach: *too unstable* local populations or/and *significant feedbacks* between local and regional dynamics.

To summarize, the presented hierarchical approach of "using cascades of models" does *not reduce* complexity. Surely, the individual models are rather simple. The entire cascade, however, covers the whole range of complexity relevant for the problem to be addressed. The major advantage of the approach is that it allows a step-wise increase of complexity and supports a hierarchical model analysis (see Chapters 3 and 4), both to the benefit of a better understanding of the dynamics. In this sense, the approach just helps to *manage* the effect of complexity. Therefore, it bridges between closeness to reality and tractability.

7.1.2 Managing biological variability: effective parameters

Even if models are generic and relatively simple compared to other models, they can show a certain complexity. Complexity can be caused, for example, by individual variability or spatial heterogeneity (in this thesis: patch individuality). In these cases, however, there are special methods for further model simplification and complexity management.

One strategy is to search for *effective parameters*. The idea is to make use of an ideal, non-structured model and to parameterize it in such a way that aspects of the dynamics of the original model are correctly reproduced. Once appropriately specified, the parameters of the non-structured model summarize all the relevant effects of biological variability covered by the original model. In this sense, these parameters are "effective".

7.1.2.1 Some examples for the search for "effective parameters"

There are some *examples* where the strategy of searching for effective parameters has been successfully applied in different fields of population ecology, for different purposes:

Example 1:

The most prominent example of an effective parameter is certainly the effective population size well-known from population genetics (e.g. Wright 1938; Lande and Barrowclough

1987; Gilpin 1991). Here, one is interested in the size of an ideal (i.e. non-structured) population which shows the same degree of heterozygocity as a given structured population. This information is important for assessing the vulnerability of the population to demographic stochasticity.

Example 2:

Several authors analyzed the outcome of population models which incorporate different sources of stochasticity (e.g., demographic / environmental stochasticity). They found that, in a wide range of situations, the simulated population dynamics can be approximated by a diffusion process, $\frac{dN}{dt} = f(N) + \sqrt{g(N)} \cdot \xi_t$ (e.g. Goodman 1987; Lande 1993; Foley 1994; Wissel *et al.* 1994). In this case, the effective parameters are given by the characteristic parameters of the drift term $f(N)$ and the diffusion term $g(N)$. One implication is the finding that demographic and environmental stochasticity result in qualitatively different diffusion terms, namely power-functions $g(N) \propto N^{\alpha}$ of the population size N where the power α characteristically depends on the type of stochasticity considered.

Example 3:

Fahse *et al.* (1998) developed an individual-based model for the population dynamics of nomadic birds in the Karoo (South Africa). This model takes the complexity of both the spatio-temporal dynamics of the landscape and the behavioral response of the individuals to them into account. In spite of this complexity, the authors found that the simulated population dynamics effectively behave as a stochastic logistic equation $\frac{dN}{dt} = \tilde{r}N(1-\frac{N}{\tilde{K}})+ \sqrt{g(N)} \cdot \xi_t$ with an effective individual growth rate $\tilde{r}$ and an effective carrying capacity $\tilde{K}$. This finding has an important methodological implication. It indicates that there is a clear protocol (namely diffusion approximation) for extracting population parameters such as $\tilde{r}$ and $\tilde{K}$ from individual-based models. This contributes to a reconciliation of classical and individual-based approaches of population modeling.

Example 4:

In the context of metapopulations, there are two similar studies on effective parameters. Both analyze the dynamics of a certain weighted mean $p_w(t) = \sum_i w_i \cdot p_i(t)$ and $p_w(t) = \sum_i w_i \cdot x_i(t)$ of the patch occupancies induced by the deterministic and stochastic spatial

Levins model, respectively, with weights w_i given by so-called patch values (Ovaskainen and Hanski 2003). In the deterministic case, the dynamics of $p_w(t)$ was found to behave as the solution of the classical Levins model $\frac{dp}{dt} = \tilde{c} \cdot p(1-p) - \tilde{\nu} \cdot p$ with effective colonization and extinction rates, $\tilde{c}$ and $\tilde{\nu}$ (Ovaskainen and Hanski 2002). In the stochastic case, the dynamics were approximated by a diffusion process $\frac{dp}{dt} = \tilde{c} \cdot p(1-p) - \tilde{\nu} \cdot p + \sqrt{\frac{\tilde{c} \cdot p(1-p) + \tilde{\nu} \cdot p}{\tilde{N}}} \cdot \xi_t$ with effective colonization and extinction rates, $\tilde{c}$ and $\tilde{\nu}$, as before and an effective number of patches $\tilde{N}$ (Ovaskainen 2002, Ovaskainen and Hanski 2004).

Example 5:
Last but not least, we shouldn't forget the example of using effective parameters in the context of metapopulations presented in this thesis (Chapter 3): Remember that, as far as the effect on the mean lifetime of a metapopulation T_m was concerned, the spatial stochastic Levins model for N patches with patch-specific colonization and extinction rates (c_{ij}, ν_i) was found to behave as the non-spatial stochastic Levins model for the same number of patches N with aggregated parameters (c_{agg}, ν_{agg}). In all the metapopulation studies mentioned, effective parameters were used in order to obtain a better understanding of the effect of spatial heterogeneity on metapopulation dynamics and persistence.

All these examples indicate that it can be generally worthwhile in population ecology to search for effective parameters and homogeneous models in order to reproduce certain aspects of the behavior of more structured models. At first sight, this looks surprising, for the following reason. On the one hand, the existence of effective parameters is an indicator for the existence of *complete mixing* in the (meta-)population considered, otherwise the use of homogeneous models would not be adequate at all. On the other hand, at least all the three metapopulation studies and the study on the nomadic birds in the Karoo (see Examples (3-5)) assumed limited dispersal of the individuals. In the result, individual interaction in these (meta-)populations is *restricted* to a certain spatial scale, i.e. it is not global. This seems to contradict the finding of having complete mixing. But note that all the individuals mentioned act as "moving reproducing units". This means that the primary effect of the individual interaction is "creation" of new individuals and new local populations, respectively, which will be the source for further interactions. In this sense, a single individual can cause a whole sequence of interactions on a much larger spatial scale. In the result, the (meta-)population becomes *effectively mixed* in the course of time, although the range of interaction of the single individuals is restricted.

As a precondition for the occurrence of "effective mixing", the sequence of interactions has to exceed a certain length, i.e. it must not break down too early. This requires that the birth rates (colonization rates) significantly exceed the death rates (extinction rates). But this condition has anyway to be met in order to ensure the occurrence of quasi-stationarity and so the applicability of the hierarchical modeling approach (see the preceding Section).

7.1.2.2 Methods for the determination of effective parameters

There are *different methods* for determining effective parameters, each having pros and cons:

Method 1: Most of the examples discussed were related to diffusion approximation. In this context, there is standard procedure of determining effective parameters which is based on *fitting* (e.g., Karlin and Taylor 1981). Here, the mean $\mu(x)$ and the variance $\sigma^2(x)$, respectively, of the simulated growth rates is plotted against the state variable x. Then the resulting plot is fitted against an appropriate drift function $f(x)$ and an appropriate diffusion function $g(x)$, respectively. The characteristic parameters of the two functions $f(x)$ and $g(x)$ give the effective parameters desired. The advantage of this procedure is that it is applicable to a wide class of (meta-)population models where the quality of the fit, however, remains to be checked in each particular case. But note that the procedure has also a disadvantage: the effective parameters resulting from fitting are purely macroscopic, i.e. they do not give explicit insight into the functional dependence on the details but merely summarize all the effects.

Method 2: As an alternative to the fitting procedure, Ovaskainen and Hanski developed an algebraic approach to diffusion approximation which is based on *eigenvalue pertubation* (Ovaskainen and Hanski 2002). In the result, they came up with formulas for the effective parameters $\tilde{c}$, $\tilde{\nu}$, and $\tilde{N}$

(Ovaskainen and Hanski 2004) discussed in Example 4. The disadvantage of this approach in comparison with the fit-based method is that it is so far only proved to be applicable to the two spatial (deterministic and stochastic) Levins models. But note that diffusion approximations generally have a limitation: they are only applicable to systems with a large number of individuals/patches. This can become critical if conservation purposes are addressed.

Method 3: As one major result of this thesis (Chapter 3), an *aggregation-based* approach to effective parameters was developed and extensively discussed (see also Frank and Wissel 2002). This approach addresses models which take individual differences or spatial heterogeneity into account (all processes are modeled by describing each individual by a separate parameter q_i). The aim is to find appropriate aggregation rules for the parameters q_i such that the original model with its parameters q_i and the homogenized version applied to the aggregated parameters q_{agg} nearly coincide in their effect on a certain target quantity Q, i.e. $Q(q_i) \approx Q^h(q_{agg})$. Since the aggregated parameters q_{agg} are explicitly expressed in terms of the original parameters q_i, they provide structural insight into the interplay between the q_i's. This has several advantages for further model analysis, especially if generalization and unification are the aim (see next Section). A further strength of the approach is that it is also applicable to (meta-) populations with small numbers of individuals/patches which are highly relevant in the context of conservation. So far, however, there is no general recipe for finding appropriate aggregation rules, that is a weakness. Nevertheless, a recommendation can be given: Standard aggregation rules (e.g. harmonic, geometric, arithmetic, or self-weighted means) can be tested regarding their ability to fit Q. Sometimes, the qualitative behavior of the system already indicates what type of aggregation is worth being considered and what type can be excluded. Remember the saturation behavior of the mean lifetime T_m in view of one-sided enlargement of a number of emigrants $\mathcal{E}_k$. This led to the conclusion that the aggregated parameter $\mathcal{E}_{agg}$ must consist of harmonic means (see Chapter 3).

For all the methods of determining effective parameters, the comparison of models (full model vs. homogeneous model plus effective parameters) was of central importance.

7.1.2.3 Implications of using effective parameters

The strategy of using effective parameters has serious implications. Firstly, it enables a *separate analysis* of all the effects caused by the interplay between the different processes included (covered by the homogeneous model) and all the effects caused by heterogeneity (covered by the effective parameters). This separation is the actual mechanism of model simplification because the two parts (homogeneous model, effective parameters) are much simpler, more tractable and better to understand than the original model. An example for the practical value is the fact that we were allowed to take the Goel and Richter-Dyn formula for the mean lifetime T_m of metapopulations in homogeneous landscapes as a basis for the derivation of a formula for the heterogeneous case (see Chapter 3). Secondly, to use effective parameters provides a *bridge to important classical models* of population theory (e.g., logistic equation, diffusion equation, Levins model) the behavior of which is widely investigated and well understood. To take a classical model as a reference is beneficial in two respects: (a) for obtaining a better understanding of more structured models, and (b) for analyzing the functioning of important principles of population theory (e.g., recovery after a disturbance, quasi-stationarity, persistence) in more realistic situations. Both aspects are important if generalization or unification are the aim.

To search for effective parameters and effectively equivalent homogeneous models is certainly a promising strategy of model simplification. But note that all the results presented only show that original and homogeneous model are effectively equivalent regarding a *particular statistical aspect* of the dynamics (e.g. the overall population size, the resulting drift and diffusion terms, the mean lifetime T_m, or any other (meta)population dynamical target quantity Q). It is an open question till now whether the functional structure of the effective parameters is robust against a change in the perspective, i.e. in the target quantity Q considered. It can be supposed that effective parameters are not “rich enough” to correctly reproduce the full structure (e.g., age- or stage distribution, spatio-temporal patterns) of the (meta-)population dynamics. They are certainly just context-dependent projections of the effect of heterogeneity. This is a matter for further research.

To conclude, there are several possibilities to combine flexibility with tractability without any loss of information. The common elements of the two approaches discussed (hierarchical model system, using effective parameters) are the separation of details/heterogeneities and the development of interfaces for coupling the separated model parts in a later stage. But note that an appropriate model structure alone is not yet a guarantee for a successful generalization of model results. It has to be combined with an appropriate model analysis.

7.2 Appropriate model analysis

So far, we were focused on model building. Now we pass on to the question of what sort of model analysis is needed if generalization and unification of model results are the aim. Before we can start to discuss particular methods of model analysis, we have to specify the sense in which the terms "generalization" and "unification" are used in this study.

In the following, we focus on structural model results such as (a) typical functional relationships, (b) trends or trade-offs, (c) the existence of threshold or optimum values, (d) the relative importance of certain factors, or (e) the functioning of a certain mechanism. To generalize a certain result means to test its robustness against changes in the values or submodels for the model parameters, changes in the level of detail, changes in central model assumptions or even in the modeling approach. This provides insight into the range and limitations of generality of the result. This information is especially important in connection with unification relevant in situations where different approaches/models exist to answer the same question. Unification means to deal with the diversity of approaches (not to reduce it!), i.e. to clarify the consequences of choosing a particular approach, to reveal interrelations between the different approaches, and to find bridges between them.

Taking this conception as a basis, one can see that aspects of generalization/unification are also addressed in this thesis. Hence, it is worthwhile to re-consider the corresponding model analyses and to reflect them methodologically. Below we present the result of this work: We assemble a list of methods which are found to be powerful in connection with generalization/unification and discuss their ranges and limitations of applicability. To demonstrate the potential of these methods, we give examples of their application.

7.2.1 Hierarchical model analysis

Tasks such as the determination of the functional relationship between a certain target quantity Q and all the model parameters or the characterization of the relative importance of a certain factor are a challenge in situations where aspects of biological variability (e.g. spatial heterogeneity, species' ecology) are taken into consideration. In these cases, an appropriate management of the inevitable complexity is crucial - not only in connection with model building (see Section 7.1), but also in connection with the model analysis.

One possibility is to organize a hierarchical model analysis that works as follows. In the first step, the model under consideration will be artificially simplified - by neglecting details, assuming homogeneity, or even excluding factors which are known to be decisive. The only aim of this step is to obtain a model which is such simple that it can be analytically solved or its dynamic behavior can be comprehensively studied by systematic parameter variation. This model will then serve as a *reference* for the further analysis. In the second step, all the formerly excluded factors will be consecutively incorporated. By contrasting the results of consecutive model versions, insight will be provided into the effect of the factor currently added and its interplay with the factors incorporated so far. The consecutive increase in the model complexity therefore goes along with a *consecutive generation of knowledge* about the dynamic behavior of the original model. This is certainly the most important advantage of a hierarchical model analysis. It also underpins the potential of following a hierarchical modeling approach. In this thesis, hierarchical model analyses have been performed in different contexts and for different purposes:

Example 1:

In connection with the deduction of the approximation formula for the mean lifetime T_m in heterogeneous landscapes (Chapter 3), hierarchical model analyses were applied two times.

Firstly, we started with assuming spatial homogeneity and excluding the correlation of extinction. The resulting reference model was found to be equivalent to a simple birth and death model for which an analytical approximation formula for T_m existed. This formula could be extended to the correlated (still homogeneous) case. Secondly, we consecutively included aspects of spatial heterogeneity. In the result, appropriate aggregation rules for the different (patch-specific) model parameters could be found. The final approximation formula resulted from the application of the homogeneous formula to the aggregation rules.

Example 2:

Hierarchical model analyses also underly the derivation of minimum conditions for long-term metapopulation persistence (Chapter 4). Here, we started with assuming spatial homogeneity and ignoring the details for arrival probability a and degree of correlation ρ. For this model, we found that two things are needed for long-term persistence: a negligible correlation and a minimum arrival probability. In the next step, a_{ij} and ρ_{ij} were related to landscape structure (d_{ij}) and species' ecology (d_a, d_ρ). In the result, $a_{ij} = e^{-d_{ij}/d_a}$ and $\rho_{ij} = e^{-d_{ij}/d_\rho}$ became coupled to each other. In the consequence, we found that long-term persistence can only be ensured if the species' dispersal range exceeds the correlation length ($d_a > d_\rho$) and no patch is inside the range of correlation of another patch ($d_{ij} > d_\rho$). These conditions are just spatial versions of the preceding homogeneous condition. They indicate that both species and landscape have to meet some requirements. To make these results available for landscape management, we condensed them in rules of thumb.

7.2.2 Combining numerical with algebraic analyses

To test the robustness of model results against changes in the model parameters usually requires extensive numerical work in the form of parameter variations. One powerful way to overcome this drawback is the combination of numerical with algebraic analyses.

To motivate this idea, we make a short excursus and consider models which are analytically solvable. These models have exact solutions which are explicitly expressed in terms of the model parameters. This allows the functional structure of the solutions to be algebraically analyzed. In the result, important structural properties and their robustness can be deduced in a mathematically rigorous way, without having to perform any numerical work. This shows that algebraic analyses represent an effective method for the generalization of model results. Compared with numerical analyses, algebraic analyses even have two advantages: firstly, they safe time and computer work, and secondly, they lead to "harder" results (mathematically rigorous deduction vs. heuristic evidence). Therefore, whenever possible, algebraic analyses should be given preference. But note that the decisive precondition for algebraic analyses is certain knowledge about the functional structure of a relevant target quantity. In the special case of analytically solvable models, this condition is automatically met. Here, the analytical solution itself is the relevant target quantity because it summarizes all the effects covered by the model.

What is happening in the case of more complex models where the relevant target quantities can be only numerically determined? Here, numerical work is certainly unavoidable. But even in this case, there are several possibilities to perform algebraic analyses and to combine them with the necessary numerical work. In the following, we give some examples for algebraic analyses in the context of the metapopulation studies performed in this thesis (Chapters 3 to 6). The didactic aim of these examples is to demonstrate (a) what structural information can be used as starting point for algebraic analyses, (b) what techniques can be applied, and (c) in what way can generalization be supported.

7.2.2.1 Benefiting from approximation formulas for the target quantities

Algebraic analyses are especially useful if approximation formulas for the relevant target quantities exist. Although the predicted values of the target quantities are not precise anymore, approximation formulas have a merit: they provide structural insight into the functional interplay between the different model parameters. In the result, the same types of algebraic analyses become applicable as in the analytical case. The following two examples give an impression about the implications. Both examples address particular aspects of (deterministic or stochastic) metapopulation persistence. In this context, target quantities such as the metapopulation capacity λ_M, the effective number of patches $\tilde{N}$, or the mean lifetime T_m are known to be relevant (see Chapter 6). As we know, for all of them, special approximation formulas exist which are expressed in terms of the (main) model parameters (e.g. extinction rates ν_i, colonization rates c_{ij}) and related quantities.

Example 1:

In Chapter 6, we were interested in understanding the effect of spatial heterogeneity on (deterministic and stochastic) metapopulation persistence. To meet this goal, we started with an analysis of the approximation formulas for the metapopulation capacity λ_M (Equation (6.5)) and the effective number of patches $\tilde{N}$ (Equation (6.16)). As the result of simple algebraic transformations, both formulas could be rewritten in terms of variances in the main model parameters $\{\nu_i, c_{ij}\}$ and related quantities $\{w_i, p_i^*\}$. These variances could be directly interpreted in terms of spatial heterogeneity. This allowed us to conclude that spatial heterogeneity has a positive effect on λ_M but a negative effect on $\tilde{N}$. Since this conclusion was drawn on the level of the main model parameters $\{\nu_i, c_{ij}\}$, it is independent of the details of the given landscape and the given species. Hence, the result is general. In the next step, we considered the (diffusion-based) approximation formula for the mean lifetime T_m (Equation (6.10)) which is expressed in terms λ_M and $\tilde{N}$. Since the effects of spatial heterogeneity on λ_M and $\tilde{N}$ were found to be counteracting, a trade-off effect on T_m could be concluded. For the same reasons as above, the existence of the trade-off effect is general again. The most important implication of these results was the finding that qualitatively different responses of λ_M (deterministic measure of persistence) and T_m (stochastic measure of persistence) to spatial heterogeneity (increase vs. trade-off) have to be expected. Whether the increasing or the decreasing part of the trade-off is dominating, however, could not be determined in general. Here, the species-specific strength of environmental noise in the local populations was found to be decisive.

Example 2:

In Chapter 5, we addressed the question of what allocation of habitat is optimum for (stochastic) metapopulation persistence if a certain configuration of patches is assumed. By analyzing the functional structure of the (aggregation-based) approximation formula for the mean lifetime T_m (Equation (6.9)), we found a Principle of Optimality for the case that the environmental noise in the local populations is moderate or strong. This Principle of Optimality says that the effect on T_m is maximum if $\sum_{j(\neq i)} c_{ij} = \sum_{j(\neq i)} c_{ji}$, i.e. there is a balance between the total colonization rate of each patch and its total chance of recolonization after extinction. The principle is completely expressed in terms of the colonization rates c_{ij}, i.e. it is independent of the details of the colonization process. In this sense, the principle is general. It is just a formal reflection of the fact that metapopulations depend on the functioning of the entire circle between "colonizing" and "becoming recolonized" if they cannot benefit from long-term local persistence.

In both examples, the results of the algebraic analyses were additionally checked by exemplary numerical analyses. In both cases, the results were confirmed (see Chapters 5 and 6). This shows the potential of having insight into the functional structure of the relevant target quantities and the value of searching for approximation formulas.

7.2.2.2 Benefiting from equation-based submodels for the model parameters

Algebraic analyses can also be performed if details have to be included, provided equation-based submodels are used for the integration. This is especially relevant if the interplay between the individuals and the landscape structure - the determinant of any landscape effect on the (meta)population dynamics - is to be taken into account. In this case, submodel equations $q = f_{a,b..}(v_s)$ for the main model parameters q are needed which are expressed in terms of spatial variables v_s and species-ecological attributes $\{a, b..\}$. This strategy of "using equation-based submodel" supports generalization and unification in several respects: It supports the determination of spatial effects on (meta)population persistence. Additionally, it allows their robustness to be tested against changes in the species-ecological attributes or even in the submodels themselves (comparison of alternative submodels). This provides new insights into key factors of metapopulation persistence.

Example:
We return to the Principle of Optimality. Obviously, a rule for the optimum allocation of habitat can only be determined if the functional dependence of the colonization rates c_{ij} on the landscape structure (esp. patch size, patch configuration) and the species' ecology (esp. dispersal behavior) is specified. We used the submodel $c_{ij} = y \cdot A_i^b \cdot a_{ij}$ where a_{ij} denotes the probability that an emigrant from patch i successfully arrives at patch j. To analyze the influence of the dispersal behavior, we made use of four different submodels

for a_{ij} (Equations (2.12), (2.13), (2.14), (2.16)) which cover different dispersal types. By taking the Principle of Optimality ($\sum_{j(\neq i)} c_{ij} = \sum_{j(\neq i)} c_{ji}$) as a basis, the optimum allocation rule could be determined algebraically, namely by solving the following system of equations:

$$\sum_{j(\neq i)} a_{ji} \cdot A_j^b = (\sum_{j(\neq i)} a_{ij}) \cdot A_i^b \tag{7.2}$$

By comparing the results for the different dispersal types (Chapter 5), we learned that (a) the optimum allocation rule is not general, (b) two situations have to be distinguished, and (c) the decisive criterion is whether competition between the patches for emigrants is caused by the relevant dispersal type. This led to ecologically differentiated rules of thumb: Without competition effect, habitat ought to be distributed uniformly. With competition effect, however, habitat ought to be distributed according to the degree of connectedness.

To work with submodels in the form of equations means to integrate details, but also to gain structural knowledge. This increases the chance of performing algebraic analyses. This also demonstrates the potential of following a hierarchical modeling approach. But note that, sometimes, submodels are only available in the form of simulation models. In this case, it is useful to look for approximation formulas for the submodel outcome. This is not hopeless, as the formula for the arrival probability a_{ij} by Heinz *et al.* (2004) demonstrates. This formula is a surrogate of an entire individual-based movement model, covers a wide range of dispersal behaviors, and represents one of the submodels for a_{ij} ("active search model"; Equation (2.16)) which was considered in the optimality study. This indicates the potential of using (meta)population dynamical landscape indices $Q^I = F_{\mu,\nu..}(v_s)$ as spatial submodels. These indices are particularly designed to describe the functional relationship between a certain (meta)population dynamical target quantity Q, the landscape structure and the species' ecology by a simple formula (for the concept, see Chapter 9).

7.2.2.3 Benefiting from the classical models of (meta)population theory

One strategy of particular importance in the context of combining numerical with algebraic analyses is the search for bridges from the relevant structurally realistic model to the classical models of (meta)population theory. The classical models are usually non-structured, analytically solvable and provide structural insight into important effects of the interplay between the relevant processes. This structural information can also be fruitful for the analysis of the more realistic model: Firstly, it can help to generate *hypotheses* which are worth to be tested. Secondly, it can give *hints for the numerical analysis* of the more complex model (which quantities ought to be analyzed and related to each other?).

Example 1:

In the case of the classical birth-and-death model, there is a close formula for the mean lifetime T_m of the population (Goel and Richter-Dyn 1974). The application of this formula to the special case of spatially homogeneous, uncorrelated metapopulations revealed that $(T_m \cdot \nu \cdot e^{-\frac{N}{c_{tot}/\nu}}) \approx \frac{(N-1)!}{N(N-1)^{N-1}} \cdot (\frac{c_{tot}}{\nu})^{N-1}$, i.e. that there is a power-like relationship between $(T_m \cdot \nu \cdot e^{-\frac{N}{c_{tot}/\nu}})$ and the total colonization ability of the local populations $\frac{c_{tot}}{\nu}$, where pre-factor and power depend on the number of patches N. This finding motivated the following rule for a regression analysis of the numerically determined values of T_m in the case of spatially homogeneous, *correlated* metapopulations (see Chapter 3): test $(T_m \cdot \nu \cdot e^{-\frac{N}{c_{tot}/\nu}})$ for a power-like dependence on $\frac{c_{tot}}{\nu}$; uncover the dependence of pre-factor and power on degree of correlation ρ and number of patches N. The test was "positive" and resulted in an extension of the approximation formula for T_m to the correlated case.

Example 2:

Another important example is diffusion approximation, i.e. the approximation of the dynamics of a fully structured population or metapopulation model with a diffusion process $\frac{dx}{dt} = f(x) + \sqrt{g(x)} \cdot \xi_t$, where the drift term corresponds to the classical logistic model $f(x) = \tilde{r}x(1 - x/\tilde{K})$ or the classical Levins model $f(x) = \tilde{c}x(1 - x) - \tilde{\nu}x$, respectively (see Examples 2, 3, and 4 in Section 7.1.3). The advantage of this approach is that the classical models provide clear rules for the numerical analysis of the simulation results: for example, plot the mean $\mu(x)$ of the simulated growth rates against the state variable x; fit the resulting $\mu(x)$-x-plot against $\tilde{r}x(1 - x/\tilde{K})$ (see also Method 1 in Section 7.1.3). In any case, this analysis provides important insights. A successful fit indicates that the (meta)population dynamics actually effectively behaves as the supposed diffusion process; the corresponding fit parameters (e.g., $\{\tilde{r}, \tilde{K}\}$) summarize all the effects of the population structure. In contrast to this, a decreasing quality of the fit indicates a deviation from a diffusion process and the emergence of extra effects of the population structure.

Example 3:

The last example is the class of finite Markov chain models with an absorbing extinct-state $(0, ..., 0)$. The dynamic behavior of these models is determined by their transition matrices. As is well-known, a simple eigensystem analysis of the transition matrices suffices to reveal the following effect: In most cases, the probability of extinction $P_{0n}(t)$ at time t shows an exponential structure, i.e. $P_{0n}(t) \approx 1 - c_n \cdot e^{-\nu \cdot t}$, where c_n is the probability of reaching quasi-stationarity from state n and ν is the extinction rate under quasi-stationarity. This structural law (a) gives insight into likelihood and consequences of reaching quasi-stationarity, (b) allows separate analyses of initial and intrinsic effects on (meta)population persistence, and (c) indicates that the initial effects are summarized in c_n, while the intrinsic effects are summarized in ν. All these components together provide a powerful framework for systematic analyses of (meta)population persistence. The structural law, however, also indicates how to proceed in situations where the (meta)population dynamics are not modeled by Markov chains but by Monte Carlo simulation models. The key is the fact that exponentiality of $P_{0n}(t) \approx 1 - c_n \cdot e^{-\nu \cdot t}$ is equivalent to linearity of $-\ln(1 - P_{0n}(t)) \approx -\ln(c_n) + \nu \cdot t$. This gives a rule for the numerical analysis of the simulation results (e.g. Stelter *et al.* 1997; Grimm and Wissel 2004): determine the relative frequency distribution for the times to extinction t_E over all simulation runs; calculate the cumulative probability of extinction $P_{0n}(t)$ for different times t; plot the corresponding $-\ln(1-P_{0n}(t))$-values against t; test the result for linearity. If $-\ln(1-P_{0n}(t)) \approx y_0 + m \cdot t$ then the decisive quantifiers of (meta)population persistence, ν and c_n, can be extracted from the slope m and the interception point y_0 with the y-axes: $\nu = m$ and $c_n = e^{-y_0}$.

This analysis is even two-in-one: firstly, a standard protocol for extracting information on (meta-)population persistence from simulation data, and secondly, a test for the applicability of the protocol (test for linearity). This protocol was already successfully applied in numerous (single-species) viability studies (e.g. Stelter *et al.* 1997; Wiegand *et al.* 1998; Grimm *et al.* 2003). But there is even a further implication: by applying the procedure to simulation data for multi-species populations, one can learn to what extent the range of applicability of this originally single-species method can be extended to the multi-species context (Stephan xx; Johst and Schöps xx; Stelter xx; Singer, in prep.)). This especially opens the possibility to separate between effects of stochasticity and effects of the species' interactions on the viability of the coupled population system.

7.2.3 Comparing modeling approaches

So far, we were concentrated on the determination of functional relationships and the analysis of their robustness to changes in parameter values or submodels. The corresponding main model was assumed to be the same. One particular problem of the recent ecological research, however, is the multitude of models and even modeling approaches which are in use to answer a certain ecological question. Therefore, unification work is needed in the sense of clarifying the consequences of choosing a particular model or modeling approach. This requires (a) to compare alternative models regarding their assumptions, definitions of central concepts (e.g. metapopulation persistence), target quantities Q considered, (b) to search for common effects and differences, and (c) to classify the conditions under which the models lead to the same conclusions and under which not.

Example:
In this thesis, the described strategy was applied to compare deterministic and stochastic metapopulation persistence (Chapter 6). We revealed that elements such as the initial conditions $\mathbf{x}_0$ or the subjective perspective of the decision-maker (time horizon t_H, accepted risk of extinction ε) are extra in the stochastic case. But we also found that, as long as the environmental noise in the subpopulations is weak, deterministic and stochastic approach coincide in the conclusions, i.e. the extra elements do not really matter. In the case of moderate or strong noise, however, the two approaches were found to differ considerably in the quantitative and qualitative results (trends, ranking orders).

7.3 Some conclusions

The results of this study give rise to some conclusions about the reconciliation of closeness to ecological realism and model tractability and the support of generalization/unification:

One important strategy is to combine hierarchical model building with hierarchical model analysis. Its major benefit is the step-wise generation of ecological understanding.

To link simulation models to ecological theory is of similar importance. While the models summarize relevant effects of ecological reality, theory provides general principles and hypotheses which can be checked for validity in the considered case. This underpins the importance of searching for "effective parameters" that relate the original model to an appropriate classical model of theoretical ecology. While the classical models code all information about the interactions between the relevant processes (2nd source of biocomplexity), the "effective parameters" code all information about the effect of biological variability (3rd source of biocomplexity). The insight into the effect of biological variability is best if the "effective parameters" are described/approximated by simple functions.

The two preceding strategies share a common idea that can be described as follows: "First subdivide, then integrate". But note that certain *preconditions* have to be met before the strategies can be applied without any loss of information. The hierarchical approach is only adequate as long as feedbacks between the organismic levels are missing. A successful search for effective parameters requires that the system is effectively mixed.

The central step towards model tractability was the *differentiation* between the different sources of biocomplexity (multitude of organismic levels; variety of factors and processes; biological variability). Each source has a specific effect on the overall system and opens a specific way to manage it. Hence, structural schemes such as those presented in Figures 7.1 and 7.2 are useful for the development of modeling strategies.

7.4 Prospects for further research

So far, we were focused on generalization/unification in the context of organismic ecology. This leads to the following questions: What is happening in situations where the ecological processes on the different organismic levels are coupled with other processes (e.g. hydrological or economic processes)? Are the presented strategies of managing complexity (e.g. hierarchical modeling, search for effective parameters) still applicable? Can the range and limitations of applicability of these strategies be characterized in terms of the dynamics of the external processes? To answer these questions is a matter of further research.

7.5 References

DeAngelis, D.L., and Gross, L.J. (eds.) 1992. Individual-based models and approaches in ecology. Chapman and Hall, New York

Drechsler, M., and C. Wissel. 1997. Separability of local and regional dynamics in metapopulations. Theoretical Population Biology 51: 9–21

Dunning, J.B., Stewart, D.J., Danielson, B.J., Noon, B.R., Root, T.L., Lamberson, R.H., and Stevens, E.E. 1995. Spatially explicit population models: current forms and future uses. *Ecological Applications* 5: 3–11

Fahse, L., Wissel, C., and Grimm, V. 1998. Reconciling classical and individual-based approaches of theoretical population ecology: a protocol to extract population parameters from individual-based models. *The American Naturalist* 152: 838–852

Foley, P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. *Conservation Biology* 8: 124-137

Frank, K., and C. Wissel. 2002. A formula for the mean lifetime of metapopulations in heterogeneous landscapes. *The American Naturalist* 159: 530 - 552

Gilpin, M. E. 1991. The effective size of metapopulations. *Biological Journal of the Linnean Society* 42: 165–175

Goodman, D. 1987. The demography of chance extinction. *In* Soulè, M.E. (ed.) Viable Populations for Conservation. Cambridge University Press, Cambridge, pp. 11–34

Goel, N. S., and N. Richter-Dyn. 1974. Stochastic Models in Biology. Academic Press, New York

Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned, and what could we learn in the future? *Ecological Modelling* 115: 129–148

Grimm, V., and Wissel, C. 2004. The intrinsic mean time to extinction: a unifying approach to analyzing persistence and viability of populations. *Oikos* 105: 501-511

Grimm, V., and Railsback, S.F. 2005. Individual-based Modeling and Ecology. Princeton University Press

Grimm, V., N. Dorndorf, F. Frey-Roos, C. Wissel, T. Wyszomirski, and W. Arnold. 2003. Modelling the role of social behavior in the persistence of the Alpine marmot *Marmota marmota*. Oikos (in press)

Heinz, S.K., Conradt, L., Wissel, C., and Frank, K. 2004. Dispersal behaviour in fragmented landscapes: deriving a practical formula for patch accessibility. *Landscape Ecology* (in press)

Karlin, S., and Taylor, H. 1981. A second course in stochastic processes. Academic Press, New York

Keilson, J. 1979. Markov Chain Models - Rarity and Exponentiality (Applied Mathematical Sciences 28). Springer Verlag, New York

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. The American Naturalist 142: 911-927

Lande, R., and G. F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. In: Soule, M.E. (ed.) Viable Populations for Conservation. Cambridge University Press, Cambridge, pp. 87–123

Ovaskainen, 0. 2002. The effective size of a metapopulation living in a heterogeneous patch network. *The American Naturalist* 160: 612–628

Ovaskainen, O., and Hanski, I. 2002. Transient dynamics in metapopulation response to pertubation. Theoretical Population Biology 61: 285–295

Ovaskainen, O., and Hanski, I. 2003. How much does an individual habitat fragment contribute to metapopulation dynamics and persistence? *Theoretical Population Biology* 64: 481-495

Ovaskainen, O., and Hanski, I. 2004. Metapopulation dynamics in highly fragmented landscapes. In: Hanski, I. and Gaggiotti, O. (eds.) Ecology, Genetics, and Evolution in Metapopulations, Academic Press, pp. 73-103

Pollett, P.K. 1995. The determination of quasistationary distributions directly from the transition rates of an absorbing Markov chain. *Mathematical Computer Modelling* 22: 279–287

Pollett, P.K. 1997. Limiting conditional distributions for metapopulation models. In: McDonald, A.D. and McAleer, L. (eds.) Proc. Int. Congr. on Modeling and Simulation, Vol. 2, Modeling and Simulation Society of Australia, Hobart, Australia, 807–812

Pulliam, H.R., Dunning, J.B., and Liu, J. 1992. Population dynamics on heterogeneous landscapes: a case study. *Ecological Applications* 2: 165–177

Stelter, C., M. Reich, V. Grimm, and C. Wissel. 1997. Modelling persistence in dynamic landscapes: lessons from a metapopulation of grasshopper *Bryodema tuberculata*. *Journal of Animal Ecology* 66: 508–518

Wiegand, T., Naves, J., Staphan, T., and Fernandez, A. 1998. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantibrica, Spain. *Ecological Monographs* 68: 539–570

Wiegand T., Moloney K., Naves J., and Knauer F. 1999. Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *The American Naturalist* 154: 605-627

Wissel, C., and S. Stöcker. 1991. Extinction of populations by random influences. *Theoretical Population Biology* 39: 315-328

Wissel, C., Stephan, Th., and Zaschke, S.-H. 1994. Modelling extinction of small populations. In: Remmert, H. (ed.) Minimum viable populations (Ecol. Studies 106). pp. 67–103

Wright, S. 1938. Size of population and breeding structure in relation to evolution. *Science* 87: 430–431

Chapter 8

Towards ecologically differentiated rules of thumb for conservational landscape management

In Part II of this thesis, we addressed a variety of important questions of metapopulation conservation management: (a) We determined a number of minimum conditions which have to be met by the landscape and the species in order to allow long-term metapopulation persistence. Additionally, we assessed and ranked the relative importance of different management strategies such as habitat connecting, but also local habitat management and desynchronization of the effects of regional stochasticity in the local populations (Chapter 4). (b) We characterized the optimum allocation of habitat in a given patch configuration (Chapter 5). (c) We assessed the sensitivity of central (especially spatial) effects on metapopulation persistence to ignoring and including stochasticity. This brought insight into the role of the approach chosen to analyze metapopulation persistence (Chapter 6). In all cases, it was possible to condense the scientific results in simple rules of thumb.

Rules of thumb are widely discussed in the conservation biological and the landscape ecological literature because they provide a powerful tool for decision-support in these fields. To see the relevance, note that it is neither useful nor is it possible to perform new detailed studies (e.g. record of empirical data, field-ecological experiments, model analyses) for each new species and each new study site considered. In such a situation, it is helpful to have tools which give at least a rough orientation for conservation management.

Different types of rules of thumb for conservation management can be distinguished. The *first type* consists of rules which are both spatially and species-ecologically neutral, i.e. they do neither take the landscape structure nor the species' ecology into account. These rules focus on the main processes of the (meta)population dynamics. Some of them rank the relative importance of the individual processes for (meta)population persistence (e.g. Drechsler and Wissel 1998; Frank and Wissel 1998; Etienne and Heesterbeek 2001). Other rules address the general effect of heterogeneity in the colonization abilities of the local populations on deterministic (Adler and Nuernberger 1995; Hanski and Ovaskainen 2000) and stochastic metapopulation persistence (Frank 2005; see also Chapter 6). The *second type* consists of rules which address important landscape structural effects on (meta)population persistence but are still species-ecologically neutral (e.g. Wilson and Willis 1975; Wilcove *et al.* 1986). These rules can be found in many text books on landscape ecology (e.g. Hansson *et al.* 1995). They allow to think in terms of spatial structure but ignore the fact that different organisms may differently respond to the landscape structure. This is a shortcoming because ignoring the species' ecology may lead to counter-productive conclusions. This drawback has been overcome by the *third type* of rules: ecologically differentiated rules of thumb for landscape management. These rules address important spatial effects but differentiate between the species' according to their sensitivity to changes in the landscape structure (e.g. Day and Possingham 1995; Weaver *et al.* 1996; Drechsler and Wissel 1998; Frank and Wissel 1998; Etienne 2002; Frank 2004, 2005; see also all the spatial rules derived in Chapters 4 to 6 of this thesis).

To attain guidance for the interpretation, assessment and evaluation of landscape structures through the eyes of a particular species from a conservational perspective is relevant for all branches of conservational landscape management beyond the metapopulation case. This leads to the question of the derivation of ecologically differentiated rules of thumb. A systematic methodology is missing so far. This motivated the present study.

In the following, we present a rough protocol for the derivation of ecologically differentiated rules of thumb for conservational landscape management. It is based on the methodological experience gained from analyzing the derivations of both the rules presented in this thesis and the rules available in the literature. Additionally, we discuss some limitations of the derivation of rules of thumb. We complete the study with general remarks on the merits of rules of thumb. We show that they have implications for ecological research as well as for different aspects of conservation management: landscape planning, the development of economic instruments, and integrated assessments. We conclude that rules of thumb provide bridges between ecology and various other disciplines involved in conservation management. We finalize with some prospects for further research.

8.1 Chances and limitations of the derivation of ecologically differentiated rules of thumb

In the following, we address methodological aspects of the derivation of ecologically differentiated rules of thumb for conservational landscape management. We develop a rough protocol and discuss some limitations of the derivation of these rules. Before we can start with the actual development work, we have to become clear about the demands on the functionality and the structure of ecologically differentiated rules of thumb:

Firstly, rules of thumb in general are usually derived in order to strengthen the ecological knowledge basis of conservation management and to support planning and decision processes in this context. Ecologically differentiated rules of thumb for conservational landscape management in particular code important information about the interplay between a certain (meta)population dynamical target quantity Q of interest and the landscape structure and the role of the species' ecology in this context. They are always of the form "If the species is of type X, then the landscape ought to be of type Y".

Secondly, rules of thumb merely aim at providing a rough orientation for conservation management. This means that they exclusively focus on qualitative key effects which are valid for a wide range of ecological situations. Consequently, they neither support any quantitative assessments nor do they give detailed guidance for any specific situation.

8.1.1 A rough protocol for the derivation of rules of thumb

Ecologically differentiated rules of thumb exist for several questions of metapopulation management. Numerous rules have been derived in Part II of this thesis (Chapters 4 to 6). Complementary rules are available from the literature (e.g. Day and Possingham 1995; Drechsler and Wissel 1998; Etienne 2002). All these rules have been derived by model analysis. In spite of all the differences in the details, their derivation followed a common scheme, i.e. a common sequence of model analysis steps. Although there is no guarantee of success, we can conclude the following *rough protocol*:

Step 1: Specify the question of conservation management to be addressed by the rule of thumb (e.g. minimum conditions for long-term (meta)population persistence, optimum conditions, setting priorities in a given variety of possible scenarios). This question both (a) influences the choice of an appropriate (meta)population dynamical target quantity Q as quantifier for the effect of the management (e.g., mean lifetime of a (meta)population T_m), and (b) determines the point of view from which the functional relationship between the target quantity Q and the landscape structure ought to be considered. The following list gives a rough orientation:

Management question to be addressed	*Characteristics to be analyzed*
Minimum conditions for persistence	`threshold values`
Optimum conditions	`optimum values / patterns`
Prioritizing in a variety of scenarios	`ranking orders`

Step 2: Choose both an appropriate (meta)population dynamical target quantity Q and an appropriate (meta)population model which can be used as a basis for the derivation of the rule of thumb desired.

Step 3: Analyze the functional relationship between the target quantity Q and the spatial factor of interest (e.g., area distribution). Determine the `optimum`[1].

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[1] For a better comprehensibility, the remaining steps of the protocol are formulated for the analysis of `optimum` values / patterns. They are also valid for the analysis of `threshold values`, `ranking orders`,

Step 4: Perform a sensitivity analysis and determine the species-ecological attributes which significantly influence the `optimum`.

Step 5: Determine the functional relationship between the `optimum` and the decisive species-ecological attributes.

Step 6: Condense the findings in verbal rules of thumb of the form "If the species is of type X, then the `optimum` is of type Y".

Step 7: Test the robustness of the rules of thumb against the addition of further details and conclude about their range and limitations of applicability.

This protocol indicates that two components of model analysis are particularly important in this context: (a) the determination/analysis of functional relationships, and (b) tests of sensitivity/robustness. These tasks have been already discussed in connection with the generalization of model results (Chapter 7). Hence, all the methods of model analysis found to be powerful in the context of generalization are also relevant for the derivation of the rules of thumb desired. This especially concerns the organization of a hierarchical model analysis (used for the rules in Chapter 4) or the combination of numerical with algebraic analyses (used for the rules in the Chapters 5 and 6). However, there are additional methodological aspects which are worth to be considered in more detail.

8.1.1.1 Choice of the target quantity Q

The first remark concerns the choice of the (meta)population dynamical *target quantity* Q. As we have already mentioned, it depends on both the goal of the conservation management planned and the management question to be answered. In connection with the support of (long-term) metapopulation persistence and the determination of minimum or optimum conditions in this context, for instance, one should be aware of the variety of target quantities in use: measures of (stochastic) persistence such as the mean lifetime T_m (Drechsler and Wissel 1997; Frank 1998, 2004; Frank and Wissel 1998; Ovaskainen 2002) or the probability of extinction $P_0(t)$ (Verboom *et al.* 1991; Day and Possingham 1995),

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or any other characteristics of the functional relationship between the target quantity Q and the landscape structure which are relevant for the management question to be addressed.

as well as measures of (deterministic) persistence such as the metapopulation capacity λ_M (Adler and Nuernberger 1994; Hanski and Ovaskainen 2000) or the basic reproduction ratio R_0 (Pooler 1987; Etienne and Heesterbeek 2000). Sometimes, however, one is interested in the relative contribution of the individual patches to the persistence of the entire metapopulation. This information is important in connection with prioritizing in reserve network design. Here, patch values w_i (Ovaskainen and Hanski 2003) ought to be analyzed and compared. Etienne and Heesterbeek (2001) considered management measures which affect a particular parameter p of the metapopulation dynamics. In order to assess and compare the effect of such measures on metapopulation persistence, they used the sensitivity measure $\Delta p \cdot \frac{\partial T_m}{\partial p}$ as a target quantity. This approach is especially powerful if the functional structure of T_m is known because, in this case, the sensitivity measure can be calculated analytically. But it also has a weakness because management measures usually do not affect one single parameter but a variety of parameters.

In any case, it is indispensable to specify the target quantity Q underlying the rules of thumb. This is needed because quantitative and qualitative results regarding the effect of the landscape structure can strongly depend on the target quantity Q chosen. Remember the comparative analysis of the results for the metapopulation capacity λ_M and the mean lifetime T_m (Chapter 6; see also Frank 2005). As we have demonstrated, spatial effects (e.g. ranking orders among alternative patch configurations) are highly sensitive to ignoring or including stochasticity in the sequence of extinction and colonization events if the environmental noise in the local populations is moderate or strong. In this case, it is strongly required to follow the stochastic approach to metapopulation persistence in order to avoid counter-productive management conclusions. Hence, it is important to know which rules of thumb are based on a stochastic measure of persistence and which are not.

8.1.1.2 Choice of an appropriate model

The demands on the functionality of rules of thumb result in a number of demands on the models which can be used as basis for the derivation of these rules.

Firstly, rules of thumb in general are to address qualitative key effects that are valid for a wide range of ecological situations. Moreover, they are to give a rough orientation for conservation management but no detailed guidance for specific cases. This indicates that *generic* models are adequate in this context (see also Chapter 7). These models take exclusively those factors into account which are essential and relevant for a wide range of cases. This makes them tractable, that is the precondition for generalization work needed.

Secondly, ecologically differentiated rules of thumb for conservational landscape management in particular are to code important information about the functional relationship between a certain (meta)population dynamical target quantity Q, the landscape structure and the species' ecology. This indicates that a (meta)population model is required which has the target quantity Q as outcome and which allows Q to be explicitly related to both the landscape structure and the species' ecology. A structural demand of particular importance is that the characteristics of landscape and species can be varied separately.

8.1.1.3 Classification of the species

A particular challenge in connection with the derivation of ecologically differentiated rules of thumb is the *classification* of the species' ecological attributes. At a first glance, it seems to be hopeless to manage the diversity of all the attributes characterizing a species. But note that there are two facts which are beneficial in this context:

Firstly, only those attributes have to be considered which are relevant for the effect of the interplay between the individuals and the landscape structure on the main metapopulation processes (extinction, colonization). On this hierarchical level, the relevant attributes are usually small in numbers and highly summarizing, i.e. they subsume a multitude of effects of the species' ecology on lower hierarchical levels. To see this, remember the submodel for the extinction rate $\nu_i = e \cdot A_i^{-x}$ which is known to be valid for a wide range of within patch dynamics where x gives an index for the strength of the environmental stochasticity in the local populations. The picture becomes even more clear if the submodel for the colonization rate for the case of active movement, $c_{ij} = y \cdot A_i^{\beta} \cdot \frac{R(d_{ij})^{N-1}}{\sum_k R(d_{ik})^{N-1}} \cdot R(d_{ij})$ with $R(d) = 1 - e^{-a \cdot e^{-b \cdot d}}$, is considered (see also Chapter 2). The parameters a and b of function $R(d)$ summarize all the effects of the individual movement behavior relevant for the colonization of a patch (e.g., step length, step mortality, perceptual range or other characteristics of movement patterns such as correlated random walks, Archimedian spirals, or loops; see Heinz *et al.* (2004)). These two summarizing parameters a and b can be used for the classification: species with the same values for a and b belong to the same type because they coincide in their response to the patch configuration. Note that this result also demonstrates that it is advantageous to follow an hierarchical approach and to use the approximation formula $a_{ij} = \frac{R(d_{ij})^{N-1}}{\sum_k R(d_{ik})^{N-1}} \cdot R(d_{ij})$ for the arrival probability a_{ij} (two summarizing attributes) as input of the metapopulation model instead of a full individual-based model (all the details of the movement behavior).

Secondly, rules of thumb usually address relative results. Attributes of the species which act as factors of proportionality for the target quantity Q, however, do not influence the relative results (see the parameters e and y in Chapter 5). This additionally diminishes the number of attributes which are relevant for the classification of the species.

8.1.1.4 Test of the robustness

As was already mentioned (Section 8.1.1.2), rules of thumb are usually based on tractable generic models. Since they shall support conservation management, all "key effects" revealed by the model analysis have to be checked for being "actual effects" or being artifacts of the underlying model. In any case, it is necessary to specify range and limitations of applicability of the rules. This directly leads to the question of the robustness of the rules against the addition of details. This was exemplarily tested for the rules of thumb for the optimum habitat allocation in the following experiment (Westphal and Frank (manus.)):

Example: An experiment for testing the robustness of rules of thumb

Remember that all the rules of thumb presented in this thesis are based on the assumptions of *circular* patches and a *centre-to-centre* measurement of patch distance (see also Chapter 2). In order to analyze the effects of an increasing spatial realism, we decided to allow *irregular* patch shapes and to move to an *edge-to-edge* measurement of patch distance. As in Chapter 5, we addressed the question of how to allocate a given total amount of restoration habitat over the patches of a given habitat network with maximum effect on metapopulation persistence. We considered a situation (passive dispersal; $c_{ij} = y \cdot A_i \cdot e^{-d_{ij}/d_a}$) where a "uniform" distribution was found to be optimum in the centre-to-centre reference case (see Chapter 5). The optimum allocation in the edge-to-edge case was determined by applying a simulated annealing algorithm (Metropolis *et al.* 1953, Kirkpatrick *et al.* 1983) where the approximation formula for the mean lifetime T_m (Chapter 3) was taken as objective function. In order to assess the chances of finding any simple rule of thumb, the T_m-value for the simulated optimum was compared with the T_m-values resulting from a number of heuristic allocation rules (e.g., attain a uniform distribution; allocate according to a certain patch criterion such as its current size or its degree of connectedness; in total 10 heuristics). We found the following results:

(a) The simulated annealing algorithm always resulted in a higher T_m-value than all the heuristics considered. (b) As long as the environmental noise in the local populations was moderate or strong, the "uniform" heuristic led to roughly the same T_m-value as the simulated optimum. (c) The weaker the environmental noise, the larger the difference in the T_m-values of the simulated optimum and the best heuristic. (d) In all cases, the "uniform" heuristic was found to be better than all the other heuristics considered.

These effects can be explained as follows: With an edge-to-edge measurement, patch shape and patch distance are no longer independent of each other. In the result, the allocation of habitat does not only affect patch size and shape, but also patch distance. Hence, there is an extra effect on the mean lifetime T_m. The simulated annealing algorithm allows an optimization of the allocation on two spatial scales: on the regional scale (which patch should get which percentage of habitat) and on the local scale (which part of a patch should be enlarged). All the heuristics considered exclusively cover the regional scale, but lack in any local optimization component. Note that the rule of thumb (uniform distribution) known from the centre-to-centre case, still has a certain predictive power, although it is not optimum anymore. After all, it was found to be the best of all the heuristics considered. Hence, it gives at least a rough orientation for the allocation management.

8.1.2 Limitations of the derivation of rules of thumb

So far, we were focused on the chances of deriving rules of thumb. We presented a rough protocol for the derivation of ecologically differentiated rules of thumb for conservational landscape management and discussed several methodological aspects. But note that approaches and methods generally have limitations of applicability. They ought to be known, especially when the resulting "products" are planned to be used in conservation management. Otherwise, there is a high risk of misuse and counter-productive conclusions. Therefore, we complete the study with some remarks on the limitations of the derivation of rules of thumb. Here, we distinguish two different levels of limitation: (a) limitations of the presented protocol, (b) limitations of the concept of rules of thumb itself.

8.1.2.1 Limitations of the presented protocol

The presented protocol is strongly dependent on the following assumption: Throughout a simulation run, the landscape structure (habitat quality, patch configuration) is constant. This indicates that there is a limitation of applicability if the landscape structure becomes *highly dynamic* as is the case if disturbances (e.g. floods, fire, land use regimes) or succession processes are important or habitat quality changes in the course of time. In these cases, however, the protocol can be correspondingly modified. Instead of considering the functional relationship between the target quantity Q and the landscape structure itself (Step 3), the relationship between Q and the characteristics of the landscape dynamics ought to be analyzed. This would result in rules of thumb for managing the landscape dynamics. In these cases, it anyway does not make sense to think about changes of a particular landscape structural element. It is anyway more appropriate to think in terms of dynamical regimes.

The presented protocol also assumes that the species-ecological model parameters are constant throughout a simulation run. But note that, as long as presence-absence metapopulation models are used, this does *not* inevitably mean that all the relevant behavioral and life-history attributes of the individuals are constant as well. To see this, remember the submodel for the extinction rate, $\nu_i = e{\cdot}A_i^{-x}$. It is known that the parameter x meets the following relationship: $x = \frac{2r_m}{\sigma^2} - 1$ (e.g. Wissel *et al.* 1994), where r_m is the mean and σ^2 the variance of the distribution of the individuals' intrinsic reproduction rates r_t that are assumed to fluctuate in a stochastic manner (White noise). This shows that parameter x is a statistical measure for the stochastic dynamics in the individuals' attributes. Hence, a constant value of x merely indicates that the dynamics in the r_t-values follow the same statistical law, i.e. are based on the same probability distribution.

8.1.2.2 Limitations of the concept of rules of thumb

There are also limitations of the concept of rules of thumb itself. This means that there situations where simple rules of thumb cannot be found anymore. This was the case in connection with the prediction of movement patterns in topographically heterogenous landscapes when the species shows a certain response to topography (Pe'er *et al.* 2005). Here, the rule of thumb "Go to the nearest summit" found to be valid in landscapes with a few summits only lost its validity when the topographical structure became too complex.

The latter example gives rise to the following supposition: The more complex the landscape structure, the lower the chance of finding rules of thumb. This would explain why numerous rules of thumb exist for metapopulations (spatial structure is given by a configuration of patches that is described by few patch variables (e.g., location, size, shape)) while, for more complex landscape structures, rules of thumb are widely missing.

To summarize, the presented findings indicate that, although there is no guarantee of success, it is worth to search for ecologically differentiated rules of thumb for landscape management. Since these rules merely aim at providing a rough orientation, it is appropriate to start with a tractable, generic model. Here, there is a high chance of finding rules of thumb which summarize the most important effects in the sense of a "caricature". If the need arises, further details can be included and the robustness of the rules can be tested.

8.2 Merits of ecologically differentiated rules of thumb

So far, we were concentrated on methodological aspects of the derivation of ecologically differentiated rules of thumb for conservational landscape management. Now we shift the focus of attention to the merits of such rules. As we have already mentioned, such rules code important information about the relationship between (meta)population persistence and the landscape structure and the role of the species' ecology in this context. Chapters

4, 5 and 6 of this thesis gave some examples and an impression about the type of information condensed in rules of thumb: (a) minimum conditions for long-term metapopulation persistence on species and landscape, (b) ranking orders among alternative management measures according to their effect on metapopulation persistence, (c) conditions for optimum habitat network design, (d) conditions under which stochasticity must be taken into account in landscape analyses to avoid counter-productive conclusions.

In the following, we demonstrate that rules of thumb of this type have serious implications for ecological research but also for several aspects of conservation management (e.g. landscape planning, development of economic instruments, integrated assessment).

8.2.1 Implications for ecological research

One result of particular importance for ecological research is the finding that we have to think in terms of *classes of species* if we want to understand the effects of the landscape on (meta)population viability or we plan measures of conservational landscape management. Each class is determined by a certain *ecological profile* (Andren 1994; Frank and Berger 1996; Grimm *et al.* 1996; Weaver *et al.* 1996; Frank and Wissel 1998; Vos *et al.* 2001), i.e. a set of ecological attributes which characterize the species' sensitivity to changes in the landscape structure. The concept of ecological profiles is used in various contexts to characterize the species' sensitivity to various critical impacts. Ecological profiles have been determined for the sensitivity to roads (road ecology, e.g. Jaeger *et al.* (2005)) and for the sensitivity to pesticides (ecotoxicology, e.g. Liess *et al.* (2005)), for example. In the first case, the profiles resulted from model analyses combined with techniques from fuzzy logics. The second case is even more interesting. Liess *et al.* searched for ecological profiles in the realm of field experiments. They found that five life history attributes characterize the sensitivity of microorganisms to pesticides in rivers. These results give rise to the following prospects for further research: Firstly, they encourage to investigate the sensitivity of species to other types of impacts/disturbances and to search for characteristic ecological profiles. Secondly, combining model-based and experimental approaches is certainly synergistic to the benefit of a better mechanistic understanding. Both activities would contribute to biodiversity research and management.

The existence of ecologically differentiated rules of thumb for landscape management also has an implication for the methodology of modeling. Note that the mentioned rules are based on models which were originally developed for (meta)population viability analyses (MPVA) of *single species.* These rules, however, are found to be valid for entire classes of species. Hence, it is worth to look for possibilities to extend the well-established methodology for MPVAs of single species (Shaffer 1981; Day and Possingham 1995; Drechsler and Wissel 1997; Frank and Wissel 1998; Burgman and Possingham 2000; Possingham *et al.* 2001; Beissinger and McCullough 2002; Ovaskainen 2002; Frank *et al.* 2003; Ovaskainen and Hanski 2004; Grimm and Wissel 2004) to classes of species.

8.2.2 Implications for conservation management

The information coded in ecologically differentiated rules of thumb is highly relevant for several aspects of conservational landscape management: landscape planning, the development of economic instruments, and the work with stakeholders (integrated assessment).

8.2.2.1 Relevance for landscape planning and habitat network design

The mentioned rules of thumb give rise to some guidelines for landscape planning activities in the realm of conservation management. Firstly, the rules indicate the need to think in terms of classes of species. Common conclusions about the effect of landscape changes on (meta)population persistence can only be drawn for species of the same ecological profile. Secondly, the rules clarify under which conditions a certain management measure is useful and worth to be considered at all. This especially concerns the strategy of "habitat connecting". We learned that asynchronous dynamics and a certain minimum stability of the local populations, but also a certain minimum dispersal ability of the species are required before habitat connecting can lead to noticeable effects on metapopulation persistence at all. This information has direct consequences for management prioritizing: if the need arises, desynchronization and stabilization of the local populations ought get a higher priority than connecting measures. Thirdly, the rules for optimum habitat network design help the planner to determine which management measures out off a variety of alternatives allow the best support of (meta)population persistence. Last but not least, the rules indicate that, in case of moderate or strong environmental noise, there is a need to take stochasticity into account in the landscape analyses. In this case, spatial effects on metapopulation persistence have been found to be highly sensitive to including or ignoring stochasticity (see the "Lessons about the effect of stochasticity" in Chapter 6). To ignore stochasticity therefore means to increase the risk of counter-productive conclusions.

8.2.2.2 Relevance for the development of economic instruments

Traditionally, conservation management is closely linked to landscape planning. Nowadays, economic aspects become increasingly important. In particular, there is an increasing interest in developing economic instruments for conservation management. These instruments have to be both ecologically effective and economically efficient. Ecologically differentiated rules of thumb can support the development work in several respects:

Firstly, these rules clarify under which conditions a certain management strategy is useful and worth to be considered at all (remember the discussion on "habitat connecting"). This information decreases the risk of investing in ineffective management activities.

Secondly, the rule of thumb in Chapter 5 reveals what area distribution is optimal for species' survival if a certain total habitat area and a certain patch configuration are assumed. Frank and Ring (1999) took this example as a basis and concluded some consequences for the ecological effectiveness of economic instruments such as incentive programs or compensation charge. They argued that the "optimum area distribution" indicates how a given budget available for the purchase of land ought to be invested to maximize the conservational effect. The mentioned rule of thumb reveals that the optimum area distribution strongly depends on the degree of connectedness of the individual patches. This shows that the effect of the purchase of land depends on where the area is enlarged. Hence, the decision about the investment of the money ought to take the spatial structure of the landscape into account. Until now, however, incentive programs and compensation charge are not spatially differentiated. This shows that rules of thumb help to determine *key factors of the ecological effectiveness of economic instruments.*

Thirdly, ecologically differentiated rules of thumb also help to clarify important *con-*

ceptual questions in connection with economic aspects of biodiversity conservation. Cost-benefit analyses are of central importance if assessments of the ecological effectiveness and economic efficiency of conservational management measures are the aim. The heart of such analyses is the utility function. It is widely discussed, however, whether spatial aspects have to be included in the utility function or not if effectiveness and efficiency of changes in the landscape structure have to be assessed (e.g. Wätzold and Drechsler 2005; Wätzold and Schwerdtner 2005). This question can be answered. Remember the analysis in Chapter 6 where we analyzed the functional relationship between the mean lifetime Tm and the total amount of habitat A_{tot} for different scenarios of area allocation. We showed that the T_m vs. A_{tot} curves for the different scenarios strongly differ between each other. But we also revealed that the ranking orders between the scenarios depend on the strength of environmental noise in the local populations (compare Figs. 6.2B and 6.3B). This indicates that correct conclusions on the ecological effect of the landscape structure can only be drawn if both the spatial structure of the habitat network and the species' ecology are taken into account. Hence, both aspects ought to be integrated in the utility function. Some remarks on how to combine spatial and species-ecological data and to integrate them in utility functions can be found in Chapter 9 on the (meta)population dynamical landscape indices.

8.2.2.3 Relevance for integrated assessment

Conservation management is characterized by multi-criteria and multi-agent decision processes, where conservational objectives compete with other interests. In the past decade, socioecological research invested a lot of efforts in developing concepts and strategies for integrated assessments, i.e. for the involvement of stakeholders in the decision processes (e.g. Kiker et al. 2001; Pahl-Wostl 2002; van der Sluis 2002). In this context, learning processes and decision-support tools are of central importance. Ecologically differentiated rules of thumb for landscape management support learning processes and decision-making. To see this, remember that these rules code important information about the relationship between species' survival and the landscape structure in a verbal way. Hence, they help to clarify the consequences of a considered scenario and to differentiate between possible alternatives. This strengthens the scientific basis and the transparency of the decision process and increases the chance of more sustainable decisions as well.

To summarize, all these arguments show that ecologically differentiated rules of thumb for landscape management provide a powerful tool for decision-support. These rules allow an integration of ecological knowledge in the interdisciplinary framework of conservation management. They provide a bridge from ecology to various other disciplines involved (e.g. landscape planning, economics, governance research, socioecology).

8.3 Prospects for further research

The results of this study allow some conclusions about prospects for further research. Firstly, in Section 8.1.2.2, we argued that the concept of rules of thumb for landscape management has a limitation if the spatial structure of the landscapes under consideration is too complex. But note the study in Chapter 9. In that Chapter, a rough protocol is presented for the derivation of (meta)population dynamical landscape indices Q^I. Such indices describe the functional relationship between a (meta)population dynamical target quantity Q of interest and the landscape structure by the mean of a simple function $F_{\mu,\nu..}(v_s)$ of few landscape variables v_s which have been found to be "effectively decisive" for Q. This protocol was found to work even for very complex landscapes (see the examples in Section 9.2.1). The decisive point is that Q is related to few spatial statistics, namely v_s, instead of to the landscape structure itself. This opens a completely new perspective: the derivation of rules of thumb for landscape management which are formulated in terms of spatial statistics. Important conditions for population persistence in spatially complex landscapes could be determined in this way. Such a strategy would be in the spirit of With and King (1999) who made important contributions to the unification of metapopulation dynamics and neutral landscape models. The suggested strategy would extend the unification work to the derivation of rules of thumb. Secondly, the integration of rules of thumb in the interdisciplinary framework of conservation management needs further attention. All these activities would contribute to further strengthening of the ecological knowledge basis for conservational landscape management.

8.4 References

Adler, F. R., and B. Nuernberger. 1994. Persistence in patchy irregular landscapes. *Theoretical Population Biology* 45: 41–75

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 76: 355-366

Beissinger, S. R., and D. R. McCullough (eds.). 2002. Population Viability Analysis. University of Chicago Press, Chicago

Burgman, M., and H. P. Possingham. 2000. Population viability analysis for conservation: the good, the bad and the undescribed. In A.G. Young, and G. M. Clarke (eds.). Genetics, Demography and Viability of Fragmented Populations, Cambridge University Press, London, 97-112

Day, J. R., and H. P. Possingham. 1995. A stochastic metapopulation model with variability in patch size and position. *Theoretical Population Biology* 48: 333-360

Drechsler, M., and C. Wissel. 1997. Separability of local and regional dynamics in metapopulations. *Theoretical Population Biology* 51: 9–21

Drechsler, M., and Wissel, C. 1998. Trade-offs between local and regional scale management of metapopulations. *Biological Conservation* 83: 31-41

Etienne, R.S. 2002. Striking the metapopulation balance: Mathematical models and methods meet metapopulation management. PhD Thesis, Wageningen University

Etienne, R.S., and Heesterbeek, J.A.P. 2000. On optimal size and number of reserves for metapopulation persistence. *Journal of Theoretical Biology* 203: 33-50

Etienne, R.S., and Heesterbeek, J.A.P. 2001. Rules of thumb for conservation of metapopulations based on a stochastic winking-patch model. *The American Naturalist* 158: 389-407

Frank, K. (1998) Optimizing a network of patchy habitats: from model results to rules of thumb for landscape management. In: Munro, N.W.P. und Willison, J.H.M. (Hrsg.) Linking Protected Areas with Working Landscapes Conserving, SAMPAA, Wolfville, Nova Scotia, 59-72

Frank, K. 2004. Ecologically differentiated rules of thumb for habitat network design – lessons from a formula. *Biodiversity and Conservation* 13: 189–206

Frank, K. 2005. Metapopulation persistence in heterogeneous landscapes: lessons about the effect of stochasticity. *The American Naturalist* 165: 374-388

Frank, K., and Berger, U. 1996. Metapopulation und Biotopverbund - eine kritische Betrachtung aus der Sicht der Modellierung. *Z. Ökologie und Naturschutz* 5: 151-160

Frank, K., and C. Wissel. 1998. Spatial aspects of metapopulation survival: from model results to rules of thumb for landscape management. *Landscape Ecology* 13: 363-379

Frank, K., and Ring, I. 1999. Model-based criteria for the effectiveness of conservation strategies: an evaluation of incentive programs in Saxony, Germany. In: Ring, I., Klauer, B., Wätzold, F. und Mansson, B. (Hrsg.) Ecological Economics, Physica Berlin, 91-106

Frank, K., Lorek, H., Kster, F., Sonnenschein, M., Wissel, C. und Grimm, V. 2003. META-X: Software for Metapopulation Viability Analysis. Springer-Verlag, Heidelberg

Grimm, V., Frank, K., Jeltsch, F., Brandl, R., Uchmanski, J., and Wissel, C. 1996. Pattern-oriented modelling in population ecology. *Science of the Total Environment* 183: 151–166

Grimm, V., and Wissel, C. 2004. The intrinsic mean time to extinction: a unifying approach to analyzing persistence and viability of populations. *Oikos* 105: 501-511

Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. *Nature* 404: 755-758

Hansson, L., Fahrig, L., and Merriam, G. (eds.) 1995. Mosaic landscapes and ecological processes. Chapman and Hall

Heinz, S.K., Conradt, L., Wissel, C., and Frank, K. 2004. Dispersal behaviour in fragmented landscapes: deriving a practical formula for patch accessibility. *Landscape Ecology* (in press)

Kiker, C.F., Milon, J.W., and Hodges A.W. 2001. Adaptive learning for science-based policy: the Everglades restoration. *Ecological Economics* 37: 403–416

Kirkpatrick, S., Gelatt, C.D. and Vecchi, M.P. (1983) Optimization by simulated annealing. *Science* 220: 671–680

Liess, M., and Von der Ohe, P.C. 2005. Analyzing effects of pesticides on invertebrate communities in streams. *Environmental Toxicology and Chemistry* (in press)

Metropolis, N.A., Rosenbluth, M., Rosenbluth, A. and Teller, E. (1953) Equation of state calculations by fast computing machines. *Journal of Chemical Physics* 21: 1087–1092

Ovaskainen, 0. 2002. The effective size of a metapopulation living in a heterogeneous patch network. *The American Naturalist* 160: 612–628

Ovaskainen, O. and Hanski, I. 2003. How much does an individual habitat fragment contribute to metapopulation dynamics and persistence? *Theoretical Population Biology* 64: 481-495

Ovaskainen, O. and Hanski, I. 2004. Metapopulation dynamics in highly fragmented landscapes. in I. Hanski, and O. Gaggiotti (eds.) Ecology, Genetics, and Evolution in Metapopulations, Academic Press, 73-103

Pahl-Wostl, C. 2002. Towards sustainability in the water sector - The importance of human actors and processes of social learning. *Aquatic Sciences* 64: 394–411

Pe'er, G., Saltz, D., and Frank, K. 2005. Virtual corridors: the concept and its implications for conservation management. *Conservation Biology* (in press)

Pooler, J. 1987. Measuring geographical accessibility: a review of current approaches and problems in the use of population potentials. *Geoforum* 18: 269–289

Possingham, H. P., D. B. Lindenmayer, and M. A. McCarthy. 2001. Population Viability Analysis. *Encyclopedia of Biodiversity* 4: 831-843

Shaffer, M.L. 1981. Minimum viable population sizes for species conservation. *Pacific Conservation Biology* 1: 39-45

van der Sluis, J.P. 2002. A way out of the credibility crisis of models used in integrated environmental assessment. *Futures* 34: 133–146

Verboom, J., Lankester, K. and Metz, J.A.J. 1991. Linking local and regional dynamics in stochastic metapopulation models. *Biol. J. Linnean Society* 42: 39–55

Wätzold, F., and Drechsler, M. 2005. Spatially uniform versus spatially heterogeneous compensation payments for biodiversity-enhancing land-use measures. *Environmental and Resource Economics* 31: 73–93

Wätzold, F., and Schwerdtner, K. 2005. Why be wasteful when preserving a valuable resource? A review article on the cost-effectiveness of European biodiversity conservation policy. *Biological Conservation* 123: 327–338

Weaver, J.L., Paquet, P.C. and Ruggiero, L.F. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. *Conservation Biology* 10: 964–976

Wilcove, D.S., McLennan, C.H. and Dobson, A.P. 1986. Habitat-fragmentation in the temperate zone. *In:* Soulé, M.E. (ed.) Conservation Biology. Sinauer, Sunderland. pp. 237–256

Wilson G.G. and Willis, E.O. 1975. Applied biogeography. *In* Cody, M.L., and Diamond, J.M. (eds.) Ecology and Evolution of Communities. Harvard University Press, Cambridge, MA. pp. 523–534

Wissel, C., Th. Stephan, and S.-H. Zaschke. 1994. Modelling extinction of small populations. In: Remmert, H. (ed.) Minimum viable populations (Ecol. Studies 106). pp. 67–103

With, K. A., and A. W. King. 1999. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13: 314–326

Chapter 9

Towards (meta)population dynamical landscape indices

Landscape indices are increasingly discussed in the landscape ecological literature. Originally, landscape indices have been developed in order to quantify landscape patterns (Romme 1982; Burrough 1986; Gustafson 1998 and references therein). This was motivated by the wish to document and to quantify changes in the landscape structure. There are now huge collections of quantitative measures of landscape patterns such as the FRAGSTATS collection (McGarigal and Marks 1995). Most of these measures, however, are ecologically neutral, i.e. they are not linked to any specific ecological process and they do not take into account that different organisms may differently respond to the landscape structure. These indices are purely descriptive and non-mechanistic. Neutral models undoubtedly have their merits as null-hypotheses (With and King 1997). Nevertheless, the mentioned lacks are shortcomings given the fact that the analysis and prediction of the effect of landscape patterns on ecological processes are core topics of landscape ecology.

This led to the wish to develop indices which allow the effect of the landscape structure on ecological processes to be predicted. The most prominent examples are certainly the indices for landscape connectivity which are commonly used for predicting the landscape effect on dispersal processes (e.g. Schippers 1996; Schumaker 1996; Tischendorf and Fahrig 2000; Tischendorf 2001; Tischendorf *et al.* 2003; Heinz *et al.* 2004). Few studies even go a step further and develop landscape indices for the prediction of landscape effects on (meta)population dynamical target quantities Q. Some examples are given in Table 9.1 (one of them is the formula T_m^a for the mean lifetime of metapopulations developed in Chapter 3 (Eqn. (3.20))). All these indices are expressed in terms of certain landscape variables and certain species-specific attributes. Their functional structure therefore gives insight into the interplay between landscape structure and species' ecology and the effect on important aspects of the dynamics and viability of (meta)populations. This indicates that the practical value of (meta)population dynamical landscape indices goes far beyond quantification and prediction. These indices especially support analyzing and obtaining a sound mechanistic understanding. Thus, they are powerful tools for (meta)population research, (meta)population viability analysis and conservational landscape management.

The mentioned potential of (meta)population dynamical landscape indices directly leads to the question of their derivation. The examples in Table 9.1 indicate that there is a high diversity of methods used for index derivations. The spectrum reaches from regression analysis and spatial statistics to algebraic analysis and eigenvalue approximation, i.e. the whole range of system analysis is covered. A systematic methodology, however, is completely missing so far. The need to fill this gap motivated the present study.

In the following, we develop a systematic approach to and a rough protocol for the derivation of (meta)population dynamical landscape indices. Throughout the development process, we pay attention to structural compatibility between the general scheme and the existing methods, especially those used for the derivation of the indices listed in Table 9.1. This ensures that approach and protocol (a) stand on a conceptually sound basis, (b) guide the development of new indices, and (c) allow as many as possible of the existing methods of index derivation to be fitted in. We also analyze the (meta)population dynamical landscape indices resulting from the presented protocol. We show that these indices have serious implications for landscape analysis and management: They go beyond the concept of "ecologically scaled landscape indices" introduced by Vos *et al.* (2001), support an ecological classification of species and the derivation of rules of thumb for landscape management as well. Finally, we show that these indices enrich the landscape-ecological framework because they support mechanistic understanding and strengthen the theoretical basis. We finish the study with some prospects for further research.

Table 9.1:

The (meta)population dynamical landscape indices considered throughout the study.

Target quantity	Landscape index	Model type	Reference
Dispersal success	PC	I	Schumaker (1996)
Arrival probability	a_{ij}^{I}	I	Heinz *et al.* (2004)
Mean population size Mean dispersal distance	$O_{GG}(r)$ $O_{GM}(r)$	I	Wiegand *et al.* (1999)
Critical traffic density	TD_{crit}^{I}	I	Tluk von Toschanowitz (2002)
Fraction of occupied patches	K_{mean}, C_{mean}	II	Vos *et al.* (2001)
Metapopulation capacity	λ_{M}^{I}	III	Hanski and Ovaskainen (2000)
Mean lifetime	T_{m}^{I}	III	Frank and Wissel (2002)

9.1 Development of a systematic approach

In the following, we develop a systematic approach to the derivation of (meta)population dynamical landscape indices. We start our work with an analysis of those landscape indices listed in Table 9.1. As we have already mentioned, these indices have been derived in different ways. In spite the differences in the methods of derivation, however, the indices share *two common properties*: Firstly, all the indices are based on a certain spatial (meta)-population model which has the target quantity Q of interest as outcome. To use such a model as departure point for the index derivation is powerful since models code important information about the landscape effects on the processes which are relevant for the target quantity Q. Secondly, all the methods used for the index derivation aim at revealing the functional relationship between the target quantity Q and the landscape structure and at describing this relationship by the mean of a simple function (the “index”).

The need to identify functional relationships reveals a principle problem: the range of methods which are suited to meet this goal strongly depends on the *degree of complexity* of the underlying model. Complex models require other methods than simpler ones. Therefore, it is useful to distinguish between models of "low/moderate" and "high" complexity and to develop the methodology for the index derivation for each case separately.

To use the degree of complexity as sole criterion for the classification of the models underlying index derivations has a serious weakness. The degree of complexity is a rather technical criterion and is hardly ecologically interpretable. Ecological understanding, however, is crucial because we have to look for methods which allow the ecological essentials of the functional relationship between the target quantity Q and the landscape structure to be preserved. Therefore, it is appropriate to go a step further and to search for an *ecological classification* of the sources of complexity which can become relevant in connection with the derivation of (meta)population dynamical landscape indices. Here, a clear answer can be given: irrespective of the organizational level (e.g., individual, population, metapopulation) and the target quantity Q of interest, the dynamical effect of the landscape structure is primarily determined on the individual level and influenced by the individuals' behavior and life history. Hence, the interplay between the individuals and the landscape is a key determinant and has to be appropriately taken into account. For the degree of complexity, however, it matters a lot whether the interplay is explicitly described or implicitly incorporated via the summary effect on the processes modeled.

For all these reasons, it is useful to classify the relevant models according to the way in which the *interplay between individuals and landscape structure* is incorporated and to distinguish between *explicit* and *implicit* cases. This classification is still simple, but allows to think in terms of ecological mechanisms. There are three prominent classes of models which cover a wide range of spatial (meta)population models (especially those underlying the indices in Table 9.1) and which fit in our classification scheme: individual-based, spatially explicit models (Class I, "explicit"), individual-based metapopulation models (Class II, "explicit"), and presence-absence metapopulation models (Class III, "implicit").

9.2 Development of a rough protocol

Now the basis is provided for passing on to the main objective of this study: the development of a rough protocol for the derivation of (meta)population dynamical landscape indices, where the attention is focused on the three model classes considered. We start with the development of a protocol for individual-based, spatially explicit models (Class I), i.e. the model class with the highest degree of complexity. We take the resulting protocol as starting point for the development work in the two remaining, less complex cases. For that, we explore the respects in which models of Class II and Class III are structurally simpler than models of Class I, search for possibilities to simplify the steps of the index derivation suggested by the protocol, and modify the protocol if necessary. We complete the work with methodological assessments of the (meta)population dynamical landscape indices listed in Table 9.1. We check whether their derivation follows the general protocol and the methods used fit in. This strengthens the confidence in the applicability of the protocol and gives a vivid impression about how to work with it in a concrete case.

9.2.1 Class I: Individual-based, spatially explicit models

In this class of models, the interplay between the individuals and the landscape structure is explicitly described that usually results in a multitude of spatial and behavioral parameters and in a simulation-based modeling approach (e.g. DeAngelis and Gross 1992; Grimm 1999; Wiegand *et al.* 1999; Grimm and Railsback 2005). The inevitable complexity impedes a mathematically rigorous determination of the entire functional relationship between the population dynamical target quantity Q of interest and all the model parameters mentioned. Hence, the “direct way” of deriving a landscape index for Q fails.

9.2.1.1 The Protocol

In the case of individual-based, spatially explicit models, there is no alternative to a heuristic, statistic-based methodology of the index derivation. The test indices belonging to this class (Table 9.1, Class I) indicate that the strategy of “searching for ecologically plausible indices and testing their reliability” is promising in this context, although there is no guarantee of success. The corresponding protocol consists of four steps:

Step 1: Attain a rough (qualitative) understanding of the functional relationship between the target quantity Q and the landscape structure by an appropriate model analysis. This includes (a) the identification of those landscape variables v_s which seem to be decisive for the target quantity Q, (b) the search for typical patterns in the functional relationship between Q and the decisive variables v_s, and (c) the analysis of the sensitivity of the shape of the Q-v_s-patterns to changes in the individuals' behavioral and life history attributes.

Step 2: Find a class of functions $F_{\mu,\nu..}(v_s)$ which is able to describe the Q-v_s-patterns found in Step 1. These functions may depend on a number of parameters (see the subscripts $\mu, \nu..$) in order to reproduce the shape of the Q-v_s-patterns. Keep this parameter set as small as possible.

Step 3: If a particular species with particular ecological attributes is considered, calibrate the $F_{\mu,\nu..}(v_s)$-function against the corresponding Q-v_s-pattern by appropriately parameterizing $\{\mu, \nu ...\}$. Calibration can be reached in different ways (e.g., regression analysis, maximum likelihood, sometimes algebraic analyses as demonstrated in Example 4). Take the calibrated function $Q^I = F_{\mu,\nu..}(v_s)$ as a "candidate" for the landscape index desired.

Step 4: Test the predictive power of Q^I for a wide range of landscape structures and ecological attributes by comparing the values predicted with the index (Q^I) with those simulated with the model (Q). The criteria for the predictive power can be different (e.g., quantitative correspondence or just correlation between Q^I and Q), depending on the aim.

This protocol gives a rough orientation for the derivation of (meta)population dynamical landscape indices which are based on individual-based models. The most crucial steps are certainly the identification of the landscape variables v_s which are decisive for the target quantity Q (Step 1) and the determination of a function $F_{\mu,\nu..}(v_s)$ which is able to describe the functional relationship between Q and v_s (Step 2). There are several ways to meet these goals. To give a vivid impression about the methodological possibilities, we demonstrate how the two tasks have been mastered in connection with the derivation of the five "individual-based" landscape indices listed in Table 9.1 (Class "I").

9.2.1.2 Some examples

Example 1: Dispersal success DS

Schumaker (1996) simulated individual movements through fragmented landscapes which were described as grids of habitat and non-habitat cells. Movement was modelled as random walk to the neighbor cells with different degrees of directionality and different probabilities of stopping per time. The target quantity of interest was the dispersal success DS, i.e. the probability that a released individual successfully arrives at any other habitat cell. Schumaker searched for an index that correlates with the dispersal success DS.

In order to find landscape variables which are decisive for the dispersal success DS, Schumaker tested nine statistical measures of habitat pattern commonly used in the landscape ecological literature: number of patches, contagion, distance to the nearest neighbor patch, patch area, core area, fractal dimension, patch perimeter, perimeter-area ratio, and shape index. He considered harmonic, geometric, arithmetic, and area-weighted means of all the measures (except of number of patches and contagion) and assessed their correlation with the dispersal success DS. Schumaker revealed that the area-weighted means of both the perimeter-area ratios ($AWPA = \frac{\sum_i P_i}{\sum_i A_i}$) and the shape indices ($AWSI = \frac{\sum_i P_i \cdot \sqrt{A_i}}{\sum_i A_i}$) correlated best with DS. Both measures, however, were found to have a weakness in distinguishing between small and large patches. This reduces their predictive power because small patches contribute less to the dispersal success than large patches. To overcome this drawback, Schumaker constructed a new statistical measure, called patch cohesion, $PC = (1 - s \cdot \frac{AWPA}{AWSI})(1 - \frac{1}{\sqrt{N}})^{-1}$ where N is the total number of cells in the grid and s the length of a cell. He tested a large variety of landscapes and found a nearly linear relationship between DS and PC, i.e. $DS \approx a \cdot PC + b$ with two fit parameters a and b.

The characteristics of the movement pattern such as the degree of directionality and the probability of stopping were merely found to influence the slope a and the interception point with the y-axis b of the DS-PC-regression-lines. This shows that, as long as one is merely interested in a high correlation, $DS^I = PC$ can be taken as an index for the dispersal success DS, irrespective of the details of the movement behavior.

Example 2: Arrival probability a_{ij}

Heinz *et al.* (2004) simulated individual movement through patchy landscapes. They considered configurations of circular habitat patches with homogeneous matrix in between and analyzed different movement patterns (correlated random walks, Archimedian spirals, Loops). The target quantities of interest were the arrival probabilities a_{ij} that an individual which starts at a certain patch i successfully arrives at a certain patch j (in contrast to Example 1 where it is only important that the individual arrives at any other patch, not at a specific one). Heinz *et al.* searched for a landscape index that allows the a_{ij}-values for all the pairs (i, j) to be predicted. Hence, there were two extra challenges: Firstly, an entire matrix of target quantities has to be handled instead of a single target quantity. Secondly, the demand on the predictive power of the index is stronger (correspondence instead of correlation between simulated and predicted values).

Since all the patches were assumed to have circular shapes, Heinz *et al.* hypothesized that the distances $\{d_{lk}\}$ between the patches are the decisive landscape variables for the arrival probabilities a_{ij}. Two observed patterns provided the basis for the actual index derivation: In two-patch landscapes, a clear sigmoidal relationship between a_{ij} and d_{ij} was detected. The movement patterns were merely found to influence the shape of the sigmoidal a_{ij}-d_{ij}-plot. This justified to fit the a_{ij}-d_{ij}-plot against a sigmoidal function given by $R(d) = 1 - e^{-a \cdot e^{-b \cdot d}}$. The two parameters a and b determine the shape of the function $R(d)$ and summarize the effects of the movement pattern assumed. In multi-patch landscapes, all the points of the a_{ij}-d_{ij}-plot were found to lie below the sigmoidal function $R(d_{ij})$ taken from the two-patch case. This reduction in a_{ij} was interpreted as an effect of an immanent competition between the patches for immigrants which is the stronger the more patches exist (individuals were assumed to stay at the first patch they reach such that they are prevented from arriving at another patch). Heinz *et al.* described this competition effect by a correction of $R(d_{ij})$ with a weighting factor $W_{ij} = \frac{R(d_{ij})^{N-1}}{\sum_{k(\neq i)} R(d_{ik})^{N-1}}$ where weighting was assumed to be according to the arrival probability $R(d_{ij})$ in the competition-free case. This led to $a^I_{ij} = W_{ij} \cdot R(d_{ij})$ as a candidate for the index desired. Systematic tests revealed a strong correspondence between the a_{ij}- and a^I_{ij}-values for all the pairs (i, j) for a wide range of landscapes and individual movement patterns.

Example 3: Population size N_s / Dispersal distance D_m

So far, we considered the consequences of one process: individual movement. Wiegand *et al.* (1999) simulated a more complex situation where individuals move through a fragmented landscape in order to find a suitable breeding site and to reproduce. Landscapes were described as grids of matrix, low-quality, and good-quality habitat cells. Movement, habitat selection and reproduction were modelled with behavioral rules which take the individuals' response to the landscape but also mechanisms such as density regulation into account. The target quantities were the number of females N_s with a source home range (a measure for the mean population size) and the mean dispersal distance D_m the individuals cover. Wiegand *et al.* searched for indices which correlate with N_s and D_m.

Starting point of the index derivation by Wiegand *et al.* were two ecologically plausible arguments: Firstly, the number of females N_s with a source home range depends on the degree of clumpedness of the good-quality habitat on a certain scale r. To see this, note that a high density of good-habitat cells results in a large number of small home ranges which, in addition, can be shared by several females. A measure for the degree of clumpedness is the spatial autocorrelation in the good-habitat cells. Secondly, the mean dispersal distance D_m depends on the degree of fragmentation of the habitat on a certain scale r. A measure for this is the correlation between good-habitat and matrix cells. These arguments justified the use of two ring statistics, $O_{GG}(r)$ and $O_{GM}(r)$, as descriptors of the landscape effects on N_s and D_m. These quantities are given by the mean density of good-habitat cells (in case of $O_{GG}(r)$) / of matrix cells (in case of $O_{GM}(r)$) in rings with radius r around each good-habitat cell. Since the exact value of the relevant spatial scale r was unknown, the two ring statistics were calculated for different values of r.

Wiegand *et al.* reported a clear linear relationship between N_s and $O_{GG}(r)$ and between D_m and $O_{GM}(r)$ for all values of r considered, different strategies of habitat selection, and different individual demands on habitat quality. Since they were merely interested in a high correlation, they took $N_s^I = O_{GG}(r)$ and $D_m^I = O_{GM}(r)$ as the landscape indices desired and calibrated them in each particular case by using the r-value which gives the sharpest linear regression. This r-value was found to be quite robust and in the order of magnitude of the home range size of the species considered.

Example 4: Critical traffic density TD_{crit}

Tluk von Toschanowitz (2001) analyzed the effect of traffic on the population viability of territorial species. She developed an individual- and grid-based simulation model which takes processes such as reproduction, individual movement and territory selection, but also factors such as sex and social status into account. Each grid-cell represented a territory which can be occupied by a group of individuals with a certain maximum group size. The grid of territories was overlayed by a network of roads with a certain traffic flow. Traffic was assumed to affect the mortality. It was assumed that each individual which crosses a road dies with a probability $1 - e^{-TD \cdot \frac{DC}{60}}$, where TD denotes the traffic density (cars per hour) and DC the duration of crossing, i.e. the time a crossing individual stays on the road. Tluk von Toschanowitz reported the existence of a critical traffic density TD_{crit} below which the population is viable but above which the probability of extinction, $P_0(500)$, rapidly increases. Because of the practical value of TD_{crit} as a yardstick for traffic management, the author searched for on index which allows TD_{crit} to be predicted.

Starting point of the index derivation was the finding that the modeled population effectively behaves as an ideal (i.e. non-structured, completely mixed) population, despite its complex dynamics. This led to the hypothesis that the critical traffic density TD_{crit} is a reflection of the well-known principle of population persistence “mortality $m <$ fecundity f”. The author took the average mortality over all grid cells, $m = m_{bas} + 2 \cdot \frac{n_R}{n_L} \cdot m_{tra}$, where m_{bas} denotes the basic mortality common for all cells, m_{tra} the additional traffic mortality for all cells adjacent to a road, n_R the number of roads and n_L the number of cells in one direction of the grid. Moreover, she took into consideration that the yearly traffic mortality is given by $m_{tra} = 1 - e^{-TD \cdot \frac{DC}{60} \cdot 12k \cdot (1-p_A)}$ where k is the number of road crossing attempts per month and p_A the probability of avoidance (returning at a road). By solving the threshold equation “$m = f$”, she got a formula for TD_{crit}:

$$TD^I_{crit} = \frac{-\ln(1 - \frac{1}{2} \cdot \frac{n_L}{n_R} \cdot (f - m_{bas}))}{\frac{DC}{60} \cdot 12k \cdot (1 - p_A)},$$

that is expressed in terms of parameters characterizing the landscape structure (n_L, n_R), the demography (f, m_{bas}), and the individuals’ crossing behavior (DC, k, p_A). Systematic tests of the predictive power of the index TD^I_{crit} revealed that, as long as the territory search of the individuals is restricted to the neighboring cells, there is a strong correspondence between the simulation-based and the index-based values, TD_{crit}^{sim} and TD_{crit}^{I}, for a wide range of parameter sets. If territory search occurs on a larger spatial scale, there is still a linear relationship between TD_{crit}^{sim} and TD_{crit}^{I} but the slope is > 1. This indicates that the index underestimates the actual value of the critical traffic density. The reason for this deviation is that the individuals' territory search induces a buffer effect because the loss of individuals (especially in the "road-territories") can be compensated by immigrants from more distant territories. This buffer effect is not covered by TD_{crit}^{I}. Nevertheless, the index has a certain practical value as a "conservative" predictor of TD_{crit}.

Two aspects were crucial for the successful index derivation. The first key was the finding that the modeled population behaves as an ideal population. This opened the possibility to make use of population theory (e.g., '$m = f$') and to work with effective (averaged) parameters (for the potential of using effective parameters, see also Section xx). The second key was the fact that the functional relationship between the traffic mortality m_{tra} and the traffic density TD was described by a formula, $m_{tra} = 1 - e^{-TD \cdot \frac{DC}{60} \cdot 12k \cdot (1-p_A)}$. In the result, TD_{crit} could be determined by solving a simple algebraic equation.

9.2.1.3 Some methodological conclusions

The examples indicate that there are at least three different ways of determining appropriate landscape variables v_s and fitting functions $F_{\mu,\nu..}()$: (a) comparative tests of arbitrary sets of landscape variables and determination of the variable which correlates best with the target quantity Q of interest (Example 1); (b) use of hypotheses about the key factors for the target quantity Q (e.g. degree of clumpedness on a scale r as a key factor for the number of females with source home ranges N_s (motivation for using ring statistics; Example 3), competition between patches for immigrants as a key mechanism for the probabilities of arrival a_{ij} (motivation for using a weighting factor W_{ij}; Example 2)); (c) application of principles of population theory in combination with the use of effective parameters (Example 4). Evidently, a *sound mechanistic understanding* of the landscape effects on the population dynamics is indispensable in these fields - especially in the two latter cases. The understanding-based construction of landscape indices has an important advantage: The resulting indices are both simple and ecologically interpretable.

9.2.2 Class II: Individual-based metapopulation models

Although being individual-based, the degree of complexity of this class of models is already partly reduced, for the following reason. By definition, the spatial structure of the landscape underlying any metapopulation is characterized as a configuration of habitat patches. Metapopulation models therefore already start with a list of landscape variables $\{v_s\}$ which describe the patch configuration (e.g. patch location, patch area, perimeter-area ratio of a patch, habitat suitability) and which are assumed to be relevant for the metapopulation dynamics and the target quantity Q of interest. The interplay between the individuals and the landscape structure is explicitly incorporated by describing the effect of the mentioned landscape variables v_s on the individual and/or the population dynamical parameters q. This is usually done by the mean of functions, i.e. $q = f_{a,b..}(v_s)$, where the function parameters "$a, b..$" summarize the effect of the species' ecology on q.

9.2.2.1 Implications for the protocol

The preceding findings have serious implications for the derivation of landscape indices Q^I. Since the models under consideration are individual-based, their degree of complexity is still too high (multitude of parameters) for a determination of the entire relationship between the target quantity Q and all the model parameters. Hence, there is no alternative to applying the heuristic Protocol presented in Section 9.2.1. However, the peculiarities of the model structure give rise to some modifications of single steps of the protocol:

Modification of Step 1: The basis of any index derivation is the identification of landscape variables v_s which seem to be decisive for the target quantity Q. In the case of spatially explicit models, this task required special analysis work (see Step 1 of the Protocol). In the case of metapopulation models, such analysis work is not needed anymore. Here, the spectrum of the potentially decisive landscape variables is already pre-defined: just take the landscape variables v_s used for the model description as a starting point.

Modification of Step 2: The model structure also gives some hints for the search for functions $F_{\mu,\nu..}(v_s)$ which can describe the relationship between Q and the v_s's (see Step 2 of the Protocol). Note that Q is completely determined by the individual and/or population dynamical parameters q and, hence, by the functions $q = f_{a,b..}(v_s)$. Therefore, it is useful to analyze the relationship between Q and $f_{a,b..}(v_s)$ instead of between Q and v_s itself. The model functions $f_{a,b..}(v_s)$ provide important "structural ingredients" for the overall index Q^I desired because they code all spatial information relevant for Q.

9.2.2.2 An example

Example: Percentage of occupied patches p^*

Vos *et al.* (2001) were interested in the landscape effects on (stochastic) metapopulation persistence. They worked with an individual-based metapopulation model and used patch area A_i and patch distance d_{ij} as descriptors of the landscape structure. In their model, area size A_i was related to the carrying capacity, $K_i = \frac{A_i}{A_0}$, which on its part was assumed to influence individual fecundity and mortality as an effect of density-regulation. A_0 denotes the species-specific area demand of a breeding unit. Patch distance d_{ij} was related to the individual arrival probability, $a_{ij} = e^{-d_{ij}/d_0}$, where d_0 denotes the mean dispersal range of the individuals. Vos *et al.* took the fraction of occupied patches p^* as measure of metapopulation persistence and searched for an appropriate landscape index p^{*I}.

Vos *et al.* based their index derivation on a standard result of metapopulation theory. They argued that the probability of a patch i being occupied mainly depends on two factors: (a) the local extinction rate ν_i in the patch that is negatively correlated with the carrying capacity $K_i = \frac{A_i}{A_0}$, and (b) the total colonization rate $C_i = \sum_{j \neq i} E_j \cdot a_{ji}$ that depends on the emigration rate $E_j = \delta \cdot A_j$ in all the other patches j and the probability of arriving at patch i, $a_{ji} = e^{-d_{ji}/d_0}$. This finding brought the authors to the idea to relate the (simulated) fraction of occupied patches p^* to the arithmetic means of both the carrying capacities, $K_{mean} = \frac{1}{N} \sum_i K_i = \frac{1}{N} \sum_i \frac{A_i}{A_0}$, and the total colonization rates, $C_{mean} = \frac{1}{N} \sum_i C_i = \delta \cdot \frac{1}{N} \sum_i \sum_{j(\neq i)} A_j \cdot e^{-d_{ji}/d_0}$. Both quantities K_{mean} and C_{mean} can be interpreted as population dynamical landscape indices because they are expressed in terms of landscape variables (A_i, d_{ij}) and species' attributes (A_0, d_0, δ). Vos *et al.* performed a logistic regression analysis of p^* with the logarithmic values $\ln(K_{mean})$ and $\ln(C_{mean})$ as explanatory variables. They reported a clear positive correlation. By transforming the corresponding regression line $\ln(\frac{p*}{1-p^*}) = \alpha + \beta \cdot \ln(K_{mean}) + \gamma \cdot \ln(C_{mean})$, they came out with the following predictor for p^*: $p^{*I} = \frac{C_{mean}^{\gamma}}{C_{mean}^{\gamma} + e^{-\alpha} \cdot K_{mean}^{-\beta}}$, where the regression coefficients α, β, and γ condense all the effects of the species' ecology which are relevant for p^*.

Vos *et al.* unfortunately did not say any word about from where they got the idea to perform a logistic regression analysis of p^* with the logarithmic values $\ln(K_{mean})$ and $\ln(C_{mean})$ as explanatory variables. It can be supposed, however, that they borrowed the idea from the classical Levins model. Here, the functional structure of p^* is well-known: $p^* = 1-(\frac{C}{\nu})^{-1}$. Therefore, $\ln(\frac{p^*}{1-p^*}) = \ln(\frac{C}{\nu}-1) \approx \ln(\frac{C}{\nu}) = -\ln(\nu)+\ln(C)$ for larger values of $\frac{C}{\nu}$. By taking the standard submodel for the extinction rate, $\nu = \epsilon \cdot K^{-x}$ (Foley 1994, Wissel *et al.* 1994), as a basis, we see that $\ln(\frac{p^*}{1-p^*}) \approx -\ln(\epsilon) + x \cdot \ln(K) + \ln(C)$. This indicates that the central principle underlying the index derivation is the assumption that the simulated metapopulation effectively behaves as an ideal, non-structured metapopulation. In this case, two well-known results from metapopulation theory (Levins model, standard submodel for extinction rate) indicate that p^* actually follows a logistic regression law with $\ln(K)$ and $\ln(C)$ as explanatory variables. Vos *et al.* inserted the arithmetic means K_{mean} and C_{mean} in order to deal with the effect of spatial heterogeneity.

9.2.2.3 Some methodological conclusions

The most important peculiarity of the index derivation in the case of individual-based metapopulation models is that structural information (e.g. landscape variables v_s, model functions $f_{a,b..}(v_s)$) from the model development can be used. This considerably simplifies the analysis work needed for the index derivation. As in the preceding case (Class I), ecological understanding is essential for the search of functions $F_{\mu,\nu..}(v_s)$ which describe the relationship between the target quantity Q and the landscape variables v_s. Here, two different sources of knowledge can be used: (a) experience gained from the model analysis, and (b) theoretical knowledge, especially on the dependence of the metapopulation dynamical quantity Q of interest on the extinction and colonization rates and on the dependence of the extinction and colonization rates on the landscape variables v_s.

9.2.3 Class III: Presence-absence metapopulation models

This class of models is mainly characterized by two things: (a) The landscape structure is given by a certain configuration of habitat patches and described by a set of patch variables $\{\mathbf{v_s} = (v_s^1, .., v_s^N)\}$, as is typical for metapopulations (see also Section 9.2.2). (b) In contrast to the individual-based cases previously considered, the interplay between the individuals and the landscape structure is not explicitly described anymore. Instead, it is implicitly taken into account via the summary effect on the essential metapopulation processes: the extinction and the colonization of patches. This is done by specifying the process parameters q (q stands for the colonization rates c_{ij}, extinction rates ν_i, degrees of correlation ρ_{ij} etc.) by the mean of functions of the patch variables, i.e. $q = f^q_{a^q, b^q..}(\mathbf{v_s})$, where the function parameters "a^q, b^q.." summarize the effects of the species' ecology on q. Examples for such functions are the widely used spatial submodels for the extinction rates $\nu_i = f^{\nu_i}_{\epsilon,x} = \epsilon \cdot A_i^{-x}$ and the colonization rates $c_{ij} = f^{c_{ij}}_{\delta,\beta,d_0} = \delta \cdot A_i^{\beta} \cdot e^{-d_{ij}/d_0}$.

9.2.3.1 Implications for the protocol

The structural properties of presence-absence metapopulation models ensure that the degree of complexity is much lower than in the preceding model classes (Class I and Class II). This is true in several respects: (a) The state space is tremendously reduced because neither the states of the individuals nor the states of the local populations are taken into account. Merely the occupancy states of the individual patches are considered. (b) Only processes on the highest organizational level (extinction/colonization of patches) are considered. In the result, there are only three types of process parameters q (colonization rates, extinction rates, degrees of correlation). (c) The sole source of model complexity is the individuality of the patches (patch-dependence of the process parameters).

The reduced model complexity increases the chance of determining the entire functional relationship between the target quantity Q and all the process parameters $\{q\}$. This has a serious implication for the derivation of metapopulation dynamical landscape indices: It provides an *alternative* to the heuristic protocol presented in Section 9.2.1:

Step 1: Uncover the functional relationship between the target quantity Q and all the process parameters $\{q\}$. Search for an approximating function F such that $Q \approx F(\{q\})$. Although there is no guarantee of success, approximating functions F can be determined in a mathematically driven (Example 1 below) or in a heuristic way (Example 2 below).

Step 2: Insert the functions $q = f^q_{a^q,b^q..}(\mathbf{v_s})$ for the process parameters q in $F(\{q\})$. The resulting expression $Q^I = F(\{f^q_{a^q,b^q..}(\mathbf{v_s})\})$ relates Q to the patch variables $\{\mathbf{v_s}\}$. Hence, it gives an appropriate landscape index for Q.

9.2.3.2 Some examples

Example 1: Metapopulation capacity λ_M

Hanski and Ovaskainen (2000) were interested in the landscape effects on (deterministic) metapopulation persistence. They used the spatial Levins model, i.e. the system of differential equations $\frac{dp_i}{dt} = (\sum_{j(\neq i)} c_{ji} \cdot p_j) \cdot (1 - p_i) - \nu_i \cdot p_i$, for simulating metapopulation dynamics. Based on this model, they came up with an iteration scheme $p_i = \frac{\sum_{j(\neq i)} c_{ji} \cdot p_j}{\sum_{j(\neq i)} c_{ji} \cdot p_j - \nu_i}$ for the stable equilibrium $(p_1^*, .., p_N^*)$. This allowed them to define metapopulation persistence as instability of the trivial solution $\mathbf{0}^* = (0, ..0)$ of this scheme. To operationalize this definition, they linearized the scheme in $\mathbf{0}^*$ and obtained the matrix $M = (m_{ij})$ with $m_{ij} = \frac{c_{ji}}{\nu_i}$ and $m_{ii} = 0$. They argued that $\mathbf{0}^*$ is instable if the leading eigenvalue λ_M of this matrix M (called metapopulation capacity) is > 1. The authors took λ_M as a measure for metapopulation persistence and searched for an appropriate landscape index λ_M^I.

The central step of the index derivation was the development of an approximation formula for λ_M. To meet this goal, the authors applied a standard result from Algebra. They used the fact that, for matrices M with non-negative entries, the leading eigenvalue λ_M equals the limit of a sequence of Rayleigh quotients, i.e. $\lambda_M = \lim_{n\to\infty} \frac{<M^{n+1}\mathbf{x},\mathbf{x}>}{<M^n\mathbf{x},\mathbf{x}>}$, for each vector $\mathbf{x} > 0$. They argued that the Rayleigh quotient $\frac{<M^2\mathbf{1},\mathbf{1}>}{<M^1\mathbf{1},\mathbf{1}>}$ for $n = 1$ and $\mathbf{x} = \mathbf{1} = (1, .., 1)$ provides already a satisfactory approximation for λ_M. This means that $\lambda_M \approx \lambda_M^I := \frac{<M^2\mathbf{1},\mathbf{1}>}{<M\mathbf{1},\mathbf{1}>} = \frac{<M\mathbf{1},M^*\mathbf{1}>}{<M\mathbf{1},\mathbf{1}>} = \frac{\sum_i(\sum_j m_{ij})\cdot(\sum_j m_{ji})}{\sum_k \sum_j m_{jk}} = \frac{\sum_i(\sum_{j(\neq i)} c_{ji}/\nu_i)\cdot(\sum_{j(\neq i)} c_{ij}/\nu_j)}{\sum_k \sum_{j(\neq k)} c_{kj}/\nu_j}$. Finally, the authors inserted the submodels $\nu_i = \epsilon \cdot A_i^{-x}$ and $c_{ij} = \delta \cdot A_i^{\beta} \cdot e^{-d_{ij}/d_0}$ in order to include the landscape structure in λ_M^I. This index derivation is mathematically driven.

Example 2: Mean lifetime T_m

Frank and Wissel (2002) were interested in landscape effects on (stochastic) metapopulation persistence. They used a spatially realistic Markov chain model for the simulation of the metapopulation dynamics. They took the mean lifetime T_m as measure for metapopulation persistence and searched for an appropriate landscape index T_m^I.

As in Example 1, the index derivation was essentially based on the development of an approximation formula for T_m (see also Chapter 3 in this thesis). The central argument was the finding that every spatially heterogeneous metapopulation with parameters (ν_i, c_{ij}) effectively behaves as a spatially homogeneous metapopulation with appropriately aggregated parameters $(\nu_{agg}, (\frac{c_{tot}}{\nu})_{agg})$. This allowed the authors to make use of the non-spatial version of their model which is equivalent to a special birth-and-death model. For this type of models, however, there is a close formula T_m^h for the mean lifetime T_m by Goel and Richter-Dyn (1974). The desired landscape index T_m^I resulted from applying this formula T_m^h to the aggregated parameters $(\nu_{agg}, (\frac{c_{tot}}{\nu})_{agg})$, i.e. $T_m^I = T_m^h(\nu_{agg}, (\frac{c_{tot}}{\nu})_{agg})$, and inserting the relevant spatial submodels for ν_i and c_{ij} (e.g., $\nu_i = \epsilon \cdot A_i^{-x}$, $c_{ij} = \delta \cdot A_i^{\beta} \cdot e^{-d_{ij}/d_0}$). The aggregation rules for $(\nu_{agg}, (\frac{c_{tot}}{\nu})_{agg})$ have been heuristically determined. The criterion for their acceptance was the ability to reproduce important (especially spatial) effects on metapopulation persistence qualitatively correctly and quantitatively sufficiently.

9.2.3.3 Some methodological conclusions

Presence-absence metapopulation models have an important advantage. The comparatively small number of states and process parameters opens the possibility to work with equation-based models (e.g., systems of differential equations, matrix models, Markov chains) instead of with simulation models. This increases the chance of applying analytical or algebraic methods for the determination of the functional relationship between the target quantity Q of interest and all the process parameters q. The two examples in the preceding section give an impression about the methodological possibilities. Example 1 demonstrates the advantage of target quantities Q which are given by eigenvalues of a matrix with non-negative entries. For such matrices, special approximation techniques exist (Perron-Frobenius theory, Rayleigh approximation). Example 2 shows the potential of searching for effective/aggregated parameters and working with birth-and-death models. These models have the merit that there are close formulas for a variety of target quantities Q (Goel and Richter-Dyn 1974): (a) mean first passage times F_{ij}, i.e. the time until the first passage of j occupied patches when starting with i occupied patches, (b) probabilities R_{ik} of reaching k occupied patches before extinction when starting with i occupied patches, (c) probabilities c_i of reaching quasi-stationarity when starting with i occupied patches, (d) probabilities h_n of having n occupied patches under quasi-stationarity. These formulas can be used as starting point for index derivations, as was done in connection with the mean lifetime T_m. The bottleneck is the determination of the effective parameters the functional structure of which may depend on the target quantity Q considered.

The effect of the interplay between the individuals and the landscape structure is exclusively incorporated via the functions $q = f^q_{a^q,b^q..}(\mathbf{v_s})$ for the process parameters q. While these functions are explicit in the landscape variables $\mathbf{v_s}$, they are implicit in the effects of the species' ecology and the individuals' behavior. These effects are summarized in the function parameters $\{a^q, b^q..\}$. This is a disadvantage because the relationship between the summarizing parameters $\{a^q, b^q..\}$ and the individual attributes of the species are not explicitly known. This hampers to think in terms of ecological mechanisms.

This drawback can be partly overcome. One way is to use functions $q = f^q_{a^q,b^q..}(\mathbf{v_s})$ which are not ad hoc but input-output surrogates of appropriate individual-based, spatially explicit submodels for the model parameters q. In this case, the functional relationship between the parameters $\{a^q, b^q..\}$ and the attributes of the species/individuals can be analyzed and understood. With other words, the main idea is to follow a hierarchical approach and to incorporate population dynamical landscape indices from lower organizational levels. The following two examples illustrate this idea. The first example is the widely used landscape index for the local extinction rate $\nu^I_i = \epsilon \cdot A_i^{-x}$. The power-like dependence of ν_i on the patch area A_i has been proven by numerous theoretical and individual-based population models (Foley 1994; Wissel *et al.* 1994). It is well understood that the function parameter x can be interpreted as an inverse measure for the strength of the environmental noise in the local populations. The second example is the landscape index for the arrival probability a_{ij} by Heinz *et al.* (2004), $a^I_{ij} = \frac{R(d_{ij})^{N-1}}{\sum_k R(d_{ik})^{N-1}} \cdot R(d_{ij})$ with

$R(d) = 1 - e^{-a \cdot e^{-b \cdot d}}$ (see also Example 2 in Section 9.2.1). As we have seen, this index is the surrogate of an individual-based movement model and the function parameters a and b summarize the effects of the individuals' movement behavior. This index can be used for specifying the colonization rate, e.g. $c_{ij} = \delta \cdot A_i^{\beta} \cdot a_{ij}^{I}$. Doing this, Heinz *et al.* (submitted) were able to show that the movement behavior has an influence on ranking orders among habitat networks regarding their effect on the mean lifetime T_m of the hosted metapopulation. This demonstrates that it is actually needed to integrate behavioral aspects into metapopulation models, otherwise there is a high risk of counter-productive conclusions. But we also see that it suffices to take the summary effect of the behavior into account.

Finally, we draw attention to another point. At first sight, one can get the impression that, in the case of presence-absence metapopulation models, ecological understanding is less important for the index derivation than in the two other cases. Analytical or algebraic techniques allow a straightforward derivation of the indices desired without requiring any ecological reflection. But note that ecological understanding is essential at an earlier stage namely when the functions $q = f^{q}_{a^q, b^q ..}(\mathbf{v_s})$ for the process parameters q are determined.

To summarize, we developed rough protocols for the derivation of (meta)population dynamical landscape indices for the three model classes considered. The developed protocols are very similar to each other and merely differ in two respects: Firstly, they differ in the need to search for landscape variables $\{v_s\}$ which seem to be decisive for the target quantity Q. In Class I (Section 9.2.1), this requires extra analysis work, while, in the Classes II (Section 9.2.2) and III (Section 9.2.3), the variables are already known from the model structure. Secondly, the protocols differ in the methods for determining functions which are able to describe the functional relationship between Q and the landscape variables $\{v_s\}$. With decreasing model complexity, there is a shift from purely heuristic-statistical methods (Classes I and II) to analytical or algebraic methods (Class III). We also showed that all the example indices listed in Table 9.1 and the methods of their derivation fit in the general scheme. The methodological analysis of these examples brought additional insights into the requirements of index derivations. We learned that ecological understanding is indispensable for the derivation of (meta)population dynamical landscape indices.

9.3 Implications of (meta)population dynamical landscape indices

So far, attention was focused on the methodology of index derivations. Now we go a step further and analyze the "outcome" of the presented protocols. We show that the resulting (meta)population dynamical landscape indices give rise to new insights with serious implications for landscape analysis and management as well as for landscape-ecological research. We finish the study with some prospects for further research.

9.3.1 Implications for landscape analysis

Regardless of the model class considered, the derived (meta)population dynamical landscape indices Q^I have the same functional structure: $Q^I = F_{\mu,\nu..}(\{v_s\})$, where $\{v_s\}$ are the landscape variables / spatial statistics found to be relevant and $\{\mu, \nu..\}$ are some function parameters. The indices represent *summarizing measures* of the effect of the complex interplay between the individuals and the landscape structure on the target quantity Q of interest. While the spatial variables v_s summarize effects of the landscape structure, the function parameters $\{\mu, \nu...\}$ summarize effects of the species' ecology. To fully understand the latter statement, remember the following: The protocol for Class III indicates that $Q^I = F(\{f^q_{a^q,b^q..}(\mathbf{v_s})\})$ where F is an approximating function for Q and $f^q_{a^q,b^q..}(\mathbf{v_s})$ are the model functions for the process parameters q. In this case, $F_{\mu,\nu..}() = F(\{f^q_{a^q,b^q..}()\})$. Hence, the function parameters $\{\mu, \nu...\}$ coincide with $\{a^q, b^q..\}$ which - per definition - describe the effect of the species' ecology on q and, hence, on Q. In the two other cases (Classes II and III), the heuristic protocol presented in Section 9.2.1. is relevant. Step 1 of this protocol indicates that the influence of the individuals' behavioral and life history attributes on the shape of the Q-v_s-pattern has to be assessed. This shape is reproduced by $F_{\mu,\nu..}()$, i.e. the type of the function (e.g. being additive, multiplicative, power-like, or logarithmic) and the function parameters $\{\mu, \nu...\}$. In this sense, $F_{\mu,\nu..}()$ provides *"species-specific, population dynamical glasses"* through which a given landscape can be assessed and interpreted in terms of its effect on the target quantity Q of interest. The overall landscape index $Q^I = F_{\mu,\nu..}(\{v_s\})$ provides a *bridge* between (meta)population dynamics and *neutral landscape models* in the sense of With and King (1999).

The concept of (meta)population dynamical landscape indices, $Q^I = F_{\mu,\nu,..}(\{v_s\})$, *goes beyond* the concept of ecologically scaled landscape indices introduced by (Vos *et al.* 2001). The idea of Vos *et al.* was to link landscape structures to ecological processes by appropriately scaling, i.e. by relating the relevant landscape characteristics (e.g. area, distance) to the spatial scale on which the modeled organisms typically act. This approach has a lot of merits, but also two serious drawbacks: Firstly, temporal scales can also be important because we are interested in the landscape effects on ecological processes. Secondly, it is often not clear what the decisive scales are. Especially in the context of population dynamics, the relevant scales often result from the interplay between the individuals and the landscape and, hence, depend on the individuals' behavior (for an illustration, see the index derivation of the arrival probability a_{ij} or the mean dispersal distance D_m (Examples 2 and 3 in Section 9.2.1)). Using $F_{\mu,\nu,..}()$ as "species-specific glasses" instead of being exclusively focussed on scaling allows the drawbacks to be partly overcome. $F_{\mu,\nu,..}()$ indicates which species-specific characteristics (namely $\{\mu, \nu, ..\}$) are actually needed for adequately reflecting the combined species-landscape effect on Q. These can be critical spatial or temporal scales, but also other characteristics (e.g. strength of environmental noise in the local populations). In this sense, the $F_{\mu,\nu,..}()$-approach is *wider, more flexible and better adapted to ecological processes* than a pure scaling-approach.

9.3.2 Implications for landscape management

The species-specific characteristics $\{\mu, \nu, ..\}$ in the (meta)population dynamical landscape indices $Q^I = F_{\mu,\nu,..}(v_s)$ usually summarize the effect of a multitude of attributes describing the individuals' behavior and life history. This has an important implication. If two species in a given landscape coincide in the species-specific glasses $F_{\mu,\nu,..}()$ then they also coincide in the landscape index $Q^I = F_{\mu,\nu,..}(v_s)$. This means that the two species show the same response to changes in the landscape structure, as far as the effect on the target quantity Q is concerned. Hence, the same recommendation for landscape management can be given for the two species. This indicates that $F_{\mu,\nu,..}()$ can be used as a basis for an *ecological classification of the species* according to their management needs (see also the discussion on the ecological profile (Grimm *et al.* 1996; Frank and Wissel 1998; Vos *et al.* 2001) or on the resilience profile of species (Weaver *et al.* 1996)). This is the same sort of classification as was used in connection with the derivation of ecologically differentiated rules of thumb for landscape management (remember Chapter 9). This indicates that the (meta)population dynamical landscape indices $Q^I = F_{\mu,\nu,..}(v_s)$ and the ecologically differentiated rules of thumb are closely linked to each other. Both together provide a powerful toolbox for the analysis and management of ecological classes of species. While the rules of thumb give a rough qualitative orientation for the management (e.g. for prioritizing), the landscape indices enable quantitative assessments of the effect of landscape changes on the (meta)population dynamical target quantity Q.

Nowadays, economic aspects become increasingly important for conservational landscape management. Management measures ought to be ecologically effective and economically efficient. This shows the relevance of cost-benefit analyses and utility functions in this context. As we have seen, the interplay between the individuals and the landscape structure is a key determinant of the (meta)population dynamical effect of any landscape changing activity. Hence, it has to be integrated in the utility function. The presented (meta)population dynamical landscape indices $Q^I = F_{\mu,\nu..}(v_s)$ provide a tool to do this. They relate landscape changing activities to the effect on the (meta)population dynamical target quantity Q which can than be evaluated by the actual utility function $U(Q)$:

$$\left.\begin{array}{l}\text{Landscape change}\\ \text{Species' ecology}\end{array}\right\} \xrightarrow{F_{\mu,\nu..}(v_s)} \begin{array}{c}\text{(Meta)population}\\ \text{dynamical}\\ \text{target quantity } Q\end{array} \xrightarrow{U(Q)} \begin{array}{c}\text{Utility}\\ U(Q)\end{array} \longrightarrow \begin{array}{c}\text{Cost-benefit}\\ \text{analysis}\end{array}$$

The resulting utility function $U(F_{\mu,\nu..}(v_s))$ is ecologically differentiated in two respects: the resulting spatial structure of the landscape and the species' sensitivity to changes in the landscape structure. It enriches the economic framework of landscape management.

9.3.3 Implications for the landscape-ecological research

(Meta)population dynamical landscape indices $Q^I = F_{\mu,\nu,..}(v_s)$ condense important information about both the interplay between the relevant processes, the role of spatial heterogeneity, temporal variability and the individuals' behavior and life-history in this context, and the overall effect on the target quantity Q. This is mechanistic information. Hence, we can conclude that (meta)population dynamical landscape indices *enrich the landscape-ecological framework* because they *support mechanistic thinking.*

A rough (qualitative) understanding of the landscape effects on the (meta)population dynamical target quantity Q of interest was the minimum condition for the derivation of an appropriate landscape index Q^I (see Step 1 of the protocol in Section 9.2.1). There are even indices where principles of population theory are used as starting point for the index derivation. To see this, remember Example 4 in Section 9.2.1.2 where the principle of population persistence 'mortality $m <$ fecundity f' was used to derive an index for the critical traffic density TD_{crit}. This shows that (meta)population dynamical landscape indices are quantitative measures of the landscape structure which stand on an ecologically sound basis. Hence, they provide a bridge between (meta)population ecology and landscape ecology. Doing so, they *strengthen the theoretical basis* of landscape ecology.

9.3.4 Implications for integrative modeling

(Meta)population dynamical landscape indices Q^I are *surrogates* of spatial (meta)population models (remember the demand that the indices have to approximate or at least to correlate with the target quantity Q produced by the model (see Step 4 of the heuristic protocol in Sec. 9.2.1)). They approximate the relationship between the landscape structure and the target quantity Q by the mean of an *input-output relation.* Such relations can be (a) integrated in more complex studies (e.g. integration of the index for the arrival probability a_{ij} in metapopulation models), (b) used as objective functions in optimization algorithms for reserve network design (remember the Example in Section 8.1.1.4), or (c) used as starting point for the development of utility functions $U(Q) = U(F_{\mu,\nu,..}(v_s))$ which allow landscape structure and species' ecology to be integrated in cost-benefit analyses in the context of conservational landscape management. Hence, (meta)population dynamical landscape indices $Q^I = F_{\mu,\nu,..}(v_s)$ open *new possibilities of integrative modeling*: To integrate the indices is a powerful alternative to integrating the underlying models.

9.4 Prospects for further research

Our study shows that (meta)population dynamical landscape indices represent a powerful tool for landscape analysis and management as well as for landscape-ecological research. Therefore, it is useful to look for possibilities to extend the presented model-based methodology of index derivation to more complex situations. (a) So far, we assumed that the spatial structure of the landscape in which the (meta)population dynamical processes take place is static. Hence, it is worth to take *landscape dynamics* into account and to analyze their influence on the landscape indices and the protocol of their derivation. A question of particular importance is the role of the rate with which the landscape changes occur. (b) The presented methodology for the derivation of (meta)population dynamical landscape indices was originally developed for the case of single species. As we have seen, the resulting indices $Q^I = F_{\mu,\nu,..}(\{v_s\})$ are valid for entire classes of species (see Section 9.3.1). Interactions between the species, however, were completely ignored so far. This directly leads to the question whether the methodology can be extended to *systems of interacting species*. Note that there are additional challenges in this case. For different species, different landscape structural elements can be relevant. Additionally, interactions between the species may completely change the spatio-temporal structure of the population dynamics. Therefore, it is not obvious what landscape structural elements are decisive for the overall dynamics. It is also questionable whether simple landscape indices can be found at all in this complex situation. The influence of type and intensity of the interaction between the species is another important aspect. A study by A. Singer (unpubl.[1]) produced promising results. He investigated the viability of populations of The Dusky Large Blue butterfly (*Maculinea nausithous*). The development of the butterflies strongly depends on interactions with their host ants and host plants. In spite the complexity (static plant distribution, dynamic ant distribution which changes under the pressure of the butterflies), Singer found a simple landscape index which strongly correlates with the mean lifetime T_m of the butterfly populations. If it would be generally possible to find landscape indices which describe the relationship between the landscape

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[1] The study is part of a PhD thesis which is in preparation. The study was supervised by me.

structure and the population dynamics of interacting species then these indices would provide a bridge between landscape ecology and community ecology. (c) Landscape indices are tools for quantifying and analyzing the effects of landscape patterns on ecological processes. It is worth to search for possibilities to develop a similar concept for assessing the effects of disturbance regimes. *Disturbance indices* certainly have to take all the relevant characteristics of a disturbance (frequency, intensity, spatial scale) but also its effect on the ecological system under consideration into account. To summarize, all these research projects would contribute to a *mechanistic approach to biodiversity research.*

9.5 References

Burrough, P.A. 1986. Principles of geographic information systems for land resources management. Oxford, Clarendon

DeAngelis, D.L., and Gross, L.J. (eds.) 1992. Individual-based models and approaches in ecology. Chapman and Hall, New York

Foley, P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. Conservation Biology 8: 124-137

Frank K., and Wissel C. 2002. A formula for the mean lifetime of metapopulations in heterogeneous landscapes. *The American Naturalist* 159: 530-552

Goel, N. S., and N. Richter-Dyn. 1974. Stochastic Models in Biology. Academic Press, New York

Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned, and what could we learn in the future? *Ecological Modelling* 115: 129–148

Grimm, V., Frank, K., Jeltsch, F., Brandl, R., Uchmanski, J., and Wissel, C. 1996. Pattern-oriented modelling in population ecology. *Science of the Total Environment* 183: 151–166

Grimm, V., and Railsback, S.F. 2005. Individual-based Modeling and Ecology. Princeton University Press

Gustafson, E.J. 1998. Quantifying landscape spatial pattern: What is the state of the art?. Ecosystems 1: 143–156

Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. *Nature* 404: 755-758

Heinz, S.K., Conradt, L., Wissel, C., and Frank, K. 2004. Dispersal behaviour in fragmented landscapes: deriving a practical formula for patch accessibility. *Landscape Ecology* (in press)

Heinz, S.K., Wissel, C., and Frank, K. The viability of metapopulations: individual dispersal behaviour matters. *Landscape Ecology* (submitted)

McGarigal, K., and Marks, B.J. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Portland (OR): USDA Forest Service, Pacific Northwestern Research Station; General Technical Report PNW-GTR-351

Romme, W.H. 1982. Fire and landscape diversity in sub-alpine forests of Yellowstone National Park. *Ecological Monographs* 52: 199–221

Schippers, P., Verboom, J., Knaapen, P., and Apeldoorn, R.C. 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. *Ecography* 19: 97–106

Schumaker, N. H. 1996. Using landscape indices to predict habitat connectivity. *Ecology* 77: 1210–1225

Tischendorf L. 2001. Can landscape indices predict ecological processes consistently? *Landscape Ecology* 16: 235-254

Tischendorf L., and Fahrig L. 2000. On the usage and measurement of landscape connectivity. *Oikos* 90: 7-19

Tischendorf L., Bender D.J., and Fahrig L. 2003. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. *Landscape Ecology* 18:41-50

Tluk von Toschanowitz, K. 2002. Der Einfluß von Straßennetz und Verkehrsfluss auf die Überlebensfähigkeit von territorialen Wildtierpopulationen: Eine Modellanalyse. Diplomarbeit Universität Osnabrück

Vos C.C., Verboom J., Opdam P.F.M., and Ter Braak C.J.F. 2001. Toward ecologically scaled landscape indices. *The American Naturalist* 157: 24-41.

Weaver, J.L., Paquet, P.C. and Ruggiero, L.F. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. *Conservation Biology* 10: 964–976

Wiegand T., Moloney K., Naves J., and Knauer F. 1999. Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *The American Naturalist* 154: 605-627.

Wissel, C., Th. Stephan, and S.-H. Zaschke. 1994. Modelling extinction of small populations. In: Remmert, H. (ed.) Minimum viable populations (Ecol. Studies 106). pp. 67–103

With, K.A. 1997. The application of neutral landscape models in conservation biology. *Conservation Biology* 11: 1069–1080

With, K.A., and King, A.W. 1997. The use and misuse of neutral landscape models in ecology. *Oikos* 79: 219–229

With, K.A., and King, A.W. 1999. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13: 314–326

Part IV

Lessons learnt

Chapter 10

The thesis at a glance

The aim of this Chapter is to give a brief overview over the thesis as a whole. This concerns (a) the general aim and relevance of the thesis, (b) some methodological challenges and the approach to master them, (c) the conception of the studies presented in Parts I to III (Chapters 2 to 9), and last but not least (d) the lessons learned from these studies.

10.1 General aim of the thesis and its relevance

The thesis addresses the subject of stochastic metapopulation persistence in spatially heterogeneous landscapes. A matter of particular interest is the interplay between landscape structure, species' ecology, and stochasticity and its effect on metapopulation persistence.

The thesis primarily aims at contributing to metapopulation theory and conservation management by the mean of modeling. This includes the development of appropriate methods of model building and analysis where necessary. The thesis additionally aims at synthesis work. This is motivated by the wish to make the experience gained in the course of the metapopulation studies applicable to other fields of environmental research. This concerns the methodology of using models for the disclosure of general principles, the development of concepts for theory and management, and the derivation of tools for decision-support. In this sense, the synthesized results go beyond the topic of metapopulation persistence and provide bridges to other disciplines of environmental research.

To analyze the functional relationship between landscape structure, species' ecology and metapopulation persistence is relevant for several reasons: (a) The interplay between spatial patterns and ecological processes is a core topic of spatial ecology. The role of stochasticity in this context is of particular interest. (b) Habitat loss and fragmentation are among the key factors of extinction for many species. The development of concepts and strategies for counteracting the negative effects of these landscape changes is urgent. A comprehensive understanding of the landscape- and species-ecological conditions of metapopulation persistence strengthens the scientific basis for the development of such strategies. (c) The derivation of model-based tools for decision-support in conservational landscape management is a general objective of applied environmental research.

10.2 Methodological challenges and the approach to master them

Theory building and management support require generalization work. This is a challenge in view of the biocomplexity caused by (a) the diversity of the organismic levels involved in metapopulation dynamics (individual, population, metapopulation processes), (b) the multitude of factors and processes interacting on each particular organismic level, and (c) biological variability (spatial heterogeneity, stochasticity, individual variability).

The thesis follows a hierarchical modeling approach to master the challenges. A main model focusing on the processes on the metapopulation level is supplemented by a cascade of submodels for integrating effects from lower levels such as the effects from the landscape structure and the species' ecology. Special methods of model analysis are developed in order to manage the complexity caused by biological variability. The main emphasis of the methodological development work, however, is placed on the support of generalization and unification and on the derivation of model-based tools for decision-support.

10.3 Conception of the individual studies

In Part I (Chapter 2), the modeling framework is developed which underlies the thesis. In addition to the main model, a collection of altenative submodels is given to cover a wide range of ecological situations. The specification of the models is supplemented by ecological justifications to the benefit of a better understanding of the model results. Finally, definition and measures of stochastic metapopulation persistence used (survival chance $S_{\mathbf{x_0}}(t)$, probability of reaching quasi-stationarity $c_{\mathbf{x_0}}$, mean lifetime T_m) are specified.

Part II (Chapters 3 to 6) is dedicated to the *analysis of important aspects of stochastic metapopulation persistence* (e.g. minimum and optimum conditions for long-term persistence; interrelation between deterministic and stochastic metapopulation persistence). Various aspects of the landscape structure (e.g. number and configuration of patches, patch size distribution, pattern of connectedness) and of the species' ecology (e.g. strength of environmental noise in the local populations, dispersal strategies) are analyzed in terms of their effect on metapopulation persistence. A matter of special interest is the role of synchrony / spatial correlation in the extinction processes. In order to meet the objectives of the different studies, special methods of model analysis are developed (e.g. hierarchical model analysis, work with non-spatial models and effective parameters, combination of numerical and algebraic analyses). In all the studies, special model-based tools for decision-support are developed (e.g. an approximation formula for the mean lifetime T_m of metapopulations, a Principle of Optimality for metapopulation persistence, various rules of thumb for landscape management) which condense the scientific results presented. Chapters 3 to 6 are mainly based on papers published in peer-reviewed journals.

The character of Part III (Chapters 7 to 9) is different. Its major aim is to make the experience gained in the course of the metapopulation studies in Part II applicable to other fields of environmental research. Therefore, Chapters 7 to 9 are primarily dedicated to *methodological reflection, review and synthesis work* on the basis of this thesis and the literature. The methodological work addresses three topics: (a) the use of models for generalization and unification under biocomplexity, (b) the derivation of ecologically differentiated rules of thumb for landscape management, and (c) the derivation of (meta)population dynamical landscape indices. The results attainable from the approaches and methods presented have implications for different fields of ecological research (e.g. community ecology, landscape ecology, road ecology, ecotoxicology) and various interdisciplinary aspects of landscape management (e.g. landscape planning, development of economic instruments, integrated assessment). Chapters 7 to 9 are unpublished so far.

10.4 Lessons learnt

In the following, we give a brief overview over central results of the thesis. Two classes of results are distinguished: (a) results which address the core topic of the thesis - metapopulation persistence - and which contribute to theory building and management support in this context, and (b) results which go beyond metapopulation persistence.

10.4.1 Contributions to metapopulation theory

Stochastic metapopulation persistence is influenced by several factors: the spatial structure of the underlying habitat network, the ecological attributes of the target species, different sorts of stochasticity, and the initial occupancy state $\mathbf{x_0}$ of the metapopulation.

The thesis aimed at obtaining a better mechanistic understanding of the relative importance of the different factors, their interplay and their overall effect on metapopulation persistence. This includes the disclosure of general principles of metapopulation persistence. The following results concern metapopulations which have reached quasi-stationarity. In this case, metapopulation persistence is independent of the initial occupancy state $\mathbf{x_0}$ and all the relevant effects are summarized in the mean lifetime T_m.

Below, we thematically group the results of the studies from Chapters 3 to 6. This "grouping" is done in order to maximize the understanding of the different persistence effects which usually have various "dimensions", i.e. depend on various factors. This has the price of a certain doubling, because the effects are discussed from different perspectives.

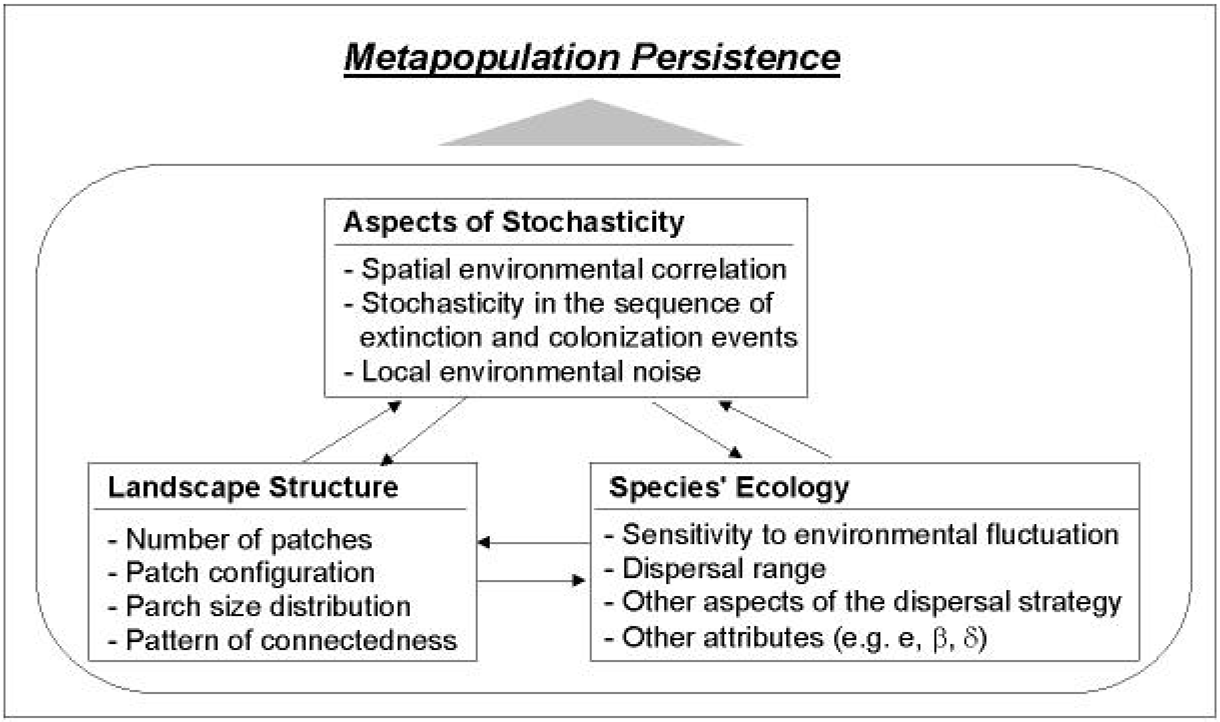

FIGURE IV.1: The central components of the persistence analyses

10.4.1.1 An approximation formula for the mean lifetime T_m

We deduced an approximation formula for the mean lifetime T_m of (quasi-stationary) metapopulations in heterogeneous landscapes (see Chapter 3). This formula is completely expressed in terms of the decisive factors of any (stochastic) metapopulation dynamics: the number of patches N, the colonization rates c_{ij}, the local extinction rates ν_i, and the degrees of correlation ρ_{ij}. The formula is "two in one": (a) a result of persistence analyses, and (b) an element of the methodology of model analysis developed in the thesis with the aim to allow *more structural* persistence analyses and generalization work.

Lesson 1 (Chapter 3):

> Although being less precise, the approximation formula T_m^a of the mean lifetime T_m has a major advantage: it provides structural insight into the functional relationship between stochastic metapopulation persistence, landscape structure, and species' ecology. The formula discloses how landscape-structural and species-ecological characteristics interact and influence the mean lifetime T_m. In the result, numerous important effects on stochastic metapopulation persistence can simply be read-off – just by analyzing the functional structure of approximation formula T_m^a.

All the Principles and Lessons presented in Section 10.4.1 have been derived by using approximation formula T_m^a in one or another form (for details, see Chapters 4 to 6).

Principle 2 (Chapter 5):

> In case of strong environmental noise in the local populations, metapopulation persistence is maximum if $\sum_{j(\neq i)} c_{ij} = \sum_{j(\neq i)} c_{ji}$ for all patches i, i.e. there is a balance between "colonizing" ($\sum_{j(\neq i)} c_{ij}$) and "becoming recolonized" ($\sum_{j(\neq i)} c_{ji}$). This balance condition reflects the fact that, in case of strong environmental noise, the local populations are short-term persistent such that the metapopulation depends on the functioning of the cycle "colonizing, going extinct, becoming recolonized".

The two Principles are general in the sense that they are independent of the details of the extinction and colonization processes, the landscape structure and the species' ecology. They provided the departure point for the derivation of some of the Lessons listed below.

10.4.1.3 Consequences of ensuring asynchrony and a minimum connectivity

In case of distance-dependent degrees of correlation (e.g. $\rho_{ij} = \mathrm{CORR}(d_{ij})$), the need to ensure both asynchrony and a certain minimum connectivity between the patches as a precondition for long-term metapopulation persistence (cf. Principle 1, Section 10.4.1.2) leads to demands on both the species' ecology and the landscape structure:

Lesson 1 (Chapter 4):

> Asynchrony and minimum connectivity are only attainable at the same time if (a) the species' dispersal range d_a is above the correlation length d_ρ (condition on the species' ecology), and (b) the distance to the nearest neighboring patches d is above d_ρ but below d_a (condition on the patch configuration). This ensures that all patches lie outside the range of correlation of any other patch but are still reachable.

Lesson 2 (Chapter 4):

> The different spatial factors in the play (correlation length d_ρ, species' dispersal range d_a, scale d and type of the patch configuration) are *not* of the same value for metapopulation persistence: As long as the species' dispersal range fails the condition required ($d_a > d_\rho$), there is no chance of obtaining long-term metapopulation persistence through a change in the landscape structure. Furthermore, an appro-

priate configuration scale is needed ($d_\rho < d < d_a$) before the configuration type becomes limiting. This leads to the following *Hierarchy of Importance*:

$$\text{dispersal range} \quad \triangleright \quad \text{configuration scale} \quad \triangleright \quad \text{configuration type.}$$

This especially indicates that only those species which cope with the spatial scale of the extinction processes d_ρ have a chance to persist in metapopulations in the long term. Hence, there is only a *class of species* which can benefit from metapopulation management (e.g. reserve network design, connecting measures) at all.

10.4.1.4 Effects of the landscape structure

The following results provide insight into (a) the role of spatial heterogeneity for (stochastic and deterministic) metapopulation persistence, (b) the effect of the interplay between spatial heterogeneity and stochasticity, (c) the spatial scale of metapopulation dynamics, (d) the role of the patch configuration, and (e) the role of the patch size distribution.

Lesson 1 (Chapters 3 and 6):

For each metapopulation with patch-specific parameters $(c_{ij}, \nu_i, \rho_{ij})$, there is a homogenous metapopulation with aggregated parameters $(c_{agg}, \nu_{agg}, \rho_{agg})$ of nearly the same mean lifetime T_m. Hence, all the *effects of spatial heterogeneity* relevant for persistence are *summarized* in the aggregated parameters $(c_{agg}, \nu_{agg}, \rho_{agg})$.

Lesson 2 (Chapter 6):

By algebraic analysis of the functional structure of the approximation formulas for the metapopulation capacity λ_M (measure of deterministic persistence) and the mean lifetime T_m (measure of stochastic persistence), we revealed the following: In the deterministic case, heterogeneity in the colonization ability of the local populations is *always advantageous* for metapopulation persistence. Hence, concentration to few strong local populations is favorable. In the stochastic case, however, heterogeneity in the colonization ability of the local populations has *always a trade-off* effect on metapopulation persistence: there is a positive effect on the strength of the local populations but a negative effect on the effective number of patches. Which effect dominates depends on the time scale of local persistence $T_l = 1/\nu_{agg}$ in relation to the time horizon t_H chosen for the analysis of metapopulation persistence. The findings are independent of the details of the colonization and extinction processes.

Lesson 3 (Chapter 6):

In case of moderate or strong environmental noise in the local populations, there are *extra effects* of the interplay between spatial heterogeneity and stochasticity in the sequence of extinction and colonization events on metapopulation persistence. In this case, local persistence is merely short-term such that the negative effect of heterogeneity on the effective number of patches becomes limiting (cf. Lesson 2). In the result, absolute and relative results (e.g. trends, ranking orders among alternative scenarios) on metapopulation persistence are highly sensitive to following the deterministic or the stochastic approach. In particular, spatial effects on metapopulation persistence can be completely different depending on whether stochasticity in the sequence of extinction and colonization events is ignored or taken into account.

Lesson 4 (Chapter 4):

The presented minimum conditions for long-term metapopulation persistence (cf. Principle 1 (Section 10.4.1.2) and Lesson 2 (Section 10.4.1.3)) merely depend on the relationship between the dispersal range d_a (or patch distance d) and the correlation length d_ρ. Thus d_ρ defines a *spatial scale* for any metapopulation dynamics and provides a yardstick for estimating the survival chance from both the species-ecological (d_a) and the landscape-structural (d_{ij}) point of view. Whenever d_ρ is neglected, a totally distorted picture of metapopulation persistence may occur.

Lesson 5 (Chapter 4):

Patch configurations are characterized by two factors: the scale (mean distance to the nearest neighbor patches) d and the type (relative arrangement of the patches). The question of *which configuration type is better* for metapopulation persistence (e.g. “Chain” or “Array”) cannot be answered in general. The answer depends on the *configuration scale* d and its relation to the correlation length d_ρ. As long as d is around or above d_ρ, an "Array" is better because of its higher arrival probability. If d is markedly below d_ρ, however, a "Chain" is better because of its lower degree of correlation. Long-term metapopulation persistence can only be obtained if $d > d_\rho$.

Lesson 6 (Chapter 5):

The question of what patch size distribution is optimum for metapopulation persistence in a habitat network with a given patch configuration cannot be answered in general. The *optimum patch size distribution* strongly depends on two factors: (a) the strength of the environmental noise in the local populations that depends on the strength of fluctuations in essential environmental factors and the species' sensitivity to them, and (b) the species' dispersal strategy: If the environmental noise in the local populations is weak then a uniform patch size distribution is optimum. If this noise is strong then the size A_i of the patches ought to correspond to their "competitiveness" DC_i (competition for dispersers), i.e. $\frac{A_i}{A_j} \approx \frac{DC_i}{DC_j}$. The competitiveness DC_i depends on the landscape structure and on the species' dispersal strategy:

- Passive dispersal: $DC_i = const = 1$ (equal competitiveness);
- Corridor-oriented dispersal: $DC_i = n_i$ (number of adjacent corridors);
- Patch-oriented dispersal (large N): $DC_i = \tilde{n}_i$ (number of nearest neighbors);
- Patch-oriented dispersal (small N): $DC_i = \sum_k R(d_{ik})^{N-1}$ (total accessibility).

Once the values of the arrival probabilities a_{ij} are known and the colonization rates are described by $c_{ij} = \delta \cdot A_i \cdot a_{ij}$, the optimum patch size distribution $A_i = p_i^{opt} \cdot A_{tot}$ can be determined by solving a simple system of linear equations (see (5.12)) derived from the Principle of Optimality (cf. Principle 2, Section 10.4.1.2).

Lesson 7 (Chapter 5):

The preceding findings contribute to the ongoing discussion about the *role of patch size variability* for metapopulation persistence. Evidently, patch size variability is only favorable if (a) the species shows strong environmental noise and a dispersal strategy that induces competition between the patches for dispersers, and (b) the "right" patches are above-average large. The latter condition reflects the fact that, in case of dispersal with competition effect, the patch size distribution has to tally with a other spatial aspects of the habitat network (e.g. patch configuration, arrangement of corridors). What aspect is relevant depends on the dispersal strategy.

10.4.1.5 Effects of the species' ecology

The analyses of the effects of the species' ecology on metapopulation persistence were focused on the following two aspects: (a) the influence of the species' ecological attributes on relative results (e.g. trends, ranking orders among alternative scenarios), and (b) minimum conditions to be met by the species to allow long-term metapopulation persistence.

Lesson 1 (Chapter 5):

Not surprisingly, the species-ecological attributes analyzed were found to influence metapopulation persistence. Some of these attributes, however, merely affect absolute results. Only few species-ecological attributes were found to influence the relative results. Examples for such attributes are: (a) the strength of the environmental noise in the local populations (depending on the species' sensitivity to fluctuations in decisive environmental factors), and (b) the species' dispersal strategy.

Lesson 2 (Chapter 6):

The *strength of environmental noise* in the local populations determines the sensitivity of the functional relationship between metapopulation persistence and landscape structure to ignoring or including stochasticity in the colonization and extinction events. It determines the occurrence of extra-effects caused by the interplay between spatial heterogeneity and stochasticity (cf. Lesson 3, Section 10.4.1.4).

Lesson 3 (Chapter 5):

The *strength of environmental noise* in the local populations influences the optimum patch size distribution in a given habitat network and its sensitivity to both the spatial structure of the network and the species' dispersal strategy (cf. Lesson 6, Section 10.4.1.4). This results from the fact that the environmental noise determines the degree of local persistence and the relative importance of successful recolonizations.

Lesson 4 (Chapter 5):

The species' *dispersal strategy* determines whether and how the optimum patch size distribution depends on the network structure (e.g. patch configuration, arrangement of corridors). However, only a few characteristics of the dispersal strategy were found to be decisive: (a) whether a competition effect between the patches for dispersers is induced, and (b) what landscape elements attract the dispersers, guide them to one patch and prevent them from moving to any other patch.

Lesson 5 (Chapter 5):

The mentioned *"competition effect"* induces additional interactions between the different elements of the spatial structure of the habitat network. This can considerably alter the effect of the landscape structure on metapopulation persistence. Therefore, the competition effect has to be taken into account, otherwise there is a high risk of counter-productive conclusions. Since actively dispersing individuals often use special landscape elements as a guide, competition effects are expected to be common. Despite this, most metapopulation models ignore the competition effect.

Lesson 6 (Chapter 4):

The *species' dispersal range* d_a determines the chance of obtaining long-term metapopulation persistence by an appropriate landscape management. Long-term persistence is only attainable if the dispersal range d_a exceeds the correlation length d_ρ.

10.4.1.6 Effects of stochasticity

Different sources of stochasticity have been analyzed in terms of their effect on metapopulation persistence: (a) environmental noise in the local populations, (b) stochasticity in the sequence of colonization and extinction events, and (c) the spatial correlation/scale of the extinction processes which can be interpreted as an indicator for regional stochasticity.

Lesson 1 (Chapter 6):

The strength of environmental noise in the local populations determines *character and extent* of the effect of stochasticity in the sequence of extinction and colonization events on metapopulation persistence. With other words, important (quantitative and even qualitative) persistence effects of one source of stochasticity can markedly depend on the strength of another source of stochasticity at another (here: lower) organizational level. This indicates that correct conclusions about metapopulation persistence can only be drawn if the interplay between different sources of stochasticity at the different levels is taken into account. This requires further research.

Lesson 2 (Chapter 6):

Spatial heterogeneity causes a decrease in the effective number of patches $\tilde{N}$. This results in an increasing number of critical initial occupancy states $\mathbf{x_0}$ which are characterized by a considerable risk of failing quasi-stationarity. These are clear symptoms of an *increasing effect of the stochasticity* in the extinction and colonization events. To see this, remember that effects of the initial occupancy states $\mathbf{x_0}$ on metapopulation persistence are completely missing in the deterministic approach.

Lesson 3 (Chapter 4):

The degree of correlation in the extinction processes limits the chance of obtaining long-term metapopulation persistence. As long as this degree is noticeable, long-term persistence is impossible. The negative effect of a simultaneous extinction of several local populations cannot be compensated by increased colonization. This is analogous to the situation in the local populations where the negative effect of strong environmental noise cannot be compensated by an increase in the carrying capacity.

These lessons provide deeper insight into the concept "metapopulation persistence" and the interplay between landscape structure, species' ecology and stochasticity in general.

10.4.2 Contributions to metapopulation management

Metapopulation management aims at obtaining long-term metapopulation persistence. Its effectiveness, however, was controversial as was mentioned in Chapter 1.

The results of this thesis support metapopulation management in several respects. Firstly, they strengthen the scientific basis of metapopulation management by providing insight into (a) minimum conditions for long-term metapopulation persistence, (b) optimum habitat network design, (c) the relative importance of various spatial factors as a basis for management prioritizing, and (d) sources of ecological uncertainty (see the Lessons in Section 10.4.1). Secondly, the scientific results have been condensed in various model-based tools for decision-support in metapopulation management.

10.4.2.1 What every decision-maker should have in mind

In the following, we assemble a number of findings every decision-maker should have in mind when designing metapopulation management. These findings help to determine (a) whether metapopulation management is useful at all in a given situation, and (b) which measures are most favorable for metapopulation persistence. They also indicate (c) under which conditions using the stochastic approach for the persistence analyses is vital.

Lesson 1 (Chapter 4):

There is only a *class of species* which can benefit from metapopulation management at all. A species can only persist as a metapopulation in the long term if its dispersal range d_a exceeds the correlation length d_ρ, i.e. the spatial scale of extinction.

Lesson 2 (Chapter 4):

Metapopulation management is only effective, i.e. leads to long-term persistence, if a number of landscape-structural preconditions are met: (a) the local populations have a certain minimum colonization potential, i.e. they are not too weak, and (b) no patch lies inside the correlation range d_ρ of any other patch.

Lesson 3 (Chapter 4):

The latter condition in Lesson 2 has serious implications for management prioritizing in different situations: (a) If patch choice in connection with habitat network design is the aim then the scale d of the resulting habitat network (mean distance to the nearest neighbors) is of higher importance than the relative arrangement of the patches. (b) If a given species in a given habitat network is considered then ensuring asynchrony in the extinction processes is a matter of priority. Desynchronization can be obtained by reducing the spatial scale d_ρ of critical anthropogenic disturbances / land use, or by diversity in the patches' exposition to critical environmental factors.

But note that the effect of desynchronization is only sufficient if d_ρ becomes smaller than both the scale d of the habitat network and the species' dispersal range d_a.

Lesson 4 (Chapter 6):

In the case of strong environmental noise in the local populations or strong spatial heterogeneity in the habitat network, it is vital to use the stochastic approach for the analyses of metapopulation persistence. This requires to take into account (a) the time-horizon of the persistence analysis t_H, (b) the accepted risk of extinction ε, and (c) the initial occupancy state $\mathbf{x_0}$, and to expect (d) extra-effects of spatial heterogeneity on absolute and relative results. Otherwise, there is a high risk of drawing counter-productive conclusions about metapopulation persistence.

Lessons 1 to 3 particularly indicate that the question of the effectiveness of habitat connecting management cannot be answered in general terms. The answer depends on the ecological attributes of the target species and the spatial structure of the habitat network.

10.4.2.2 Model-based tools for decision-support beyond computer programs

Models support conservation management in several aspect: They allow (a) ecological effects to be quantified, (b) alternative scenarios to be simulated, compared and ranked according to their ecological effect, (c) key factors of persistence and sources of uncertainty to be identified etc. A decision-maker, however, can only benefit from a model if he has access to an implemented version of the model (e.g. computer program) or to special tools which allow the same conclusions to be drawn as the original model.

In the thesis, various model-based tools for decision-support in metapopulation management have been derived. These tools represent alternatives to using software. Each tool has a special range of applicability, special pros and special cons.

Lesson 1 (Chapters 3 to 6):

The *approximation formula* T_m^a for the mean lifetime (see Chapter 3) is a powerful tool for decision-support: Firstly, it allows the decisive measure of metapopulation persistence - the mean lifetime T_m - to be predicted on a direct way, i.e. without having to resort to extensive simulations. Secondly and even more important, it provides a “tool for developing tools for decision-support”. This is meant in the sense that important structural information can simply be extracted by analyzing the functional structure of the approximation formula T_m^a. This enabled us to disclose a Principle of Optimality, a Hierarchy of Importance, as well as various Rules of Thumb - each being a tool for decision-support on its part (cf. Lessons 2 to 4).

Lesson 2 (Chapter 5):

The *Principle of Optimality* ($\sum_{j(\neq i)} c_{ij} = \sum_{j(\neq i)} c_{ji}$ for all i; cf. Principle 2 in Section 10.4.1.2) provides a tool for determining the optimum patch size distribution in the case of strong environmental noise in the local populations. If the colonization rates are described by $c_{ij} = \delta \cdot A_i \cdot a_{ij}$ and the patch areas by $A_i = p_i \cdot A_{tot}$ where A_{tot} is the total amount of habitat and p_i the percentage of habitat allocated to patch i, then the system of balance equations $\sum_{j(\neq i)} c_{ij} = \sum_{j(\neq i)} c_{ji}$ simplifies to a system of linear equations $(-\sum_{j(\neq i)} a_{ij}) \cdot p_i + \sum_{j(\neq i)} a_{ji} \cdot p_j = 0$ in the p_j's (see (5.12)). Perron-Frobenius theory indicates that this system of linear equations has a uniquely determined (up to a scaling factor) solution with non-negative entries q_i. The optimum patch size distribution desired results from $A_i = \frac{q_i}{q_1+..+q_N} \cdot A_{tot}$.

Undoubtedly, the optimum itself is not attainable in most cases. Nevertheless, the information summarized in the optimum is highly relevant for metapopulation management. The optimum patch size distribution, for instance, indicates in which direction ought a habitat network be changed to maximize the ecological benefit, i.e. which patches ought be enlarged in the realm of habitat restoration measures.

Lesson 3 (Chapter 4):

The *Hierarchy of Importance* among the different spatial factors of metapopulation persistence revealed (cf. Lesson 2 in Section 10.4.1.3) is a useful tool for setting management priorities. The hierarchy indicates that a change in a certain factor does not have any considerable effect on metapopulation persistence as long as not all conditions governing factors “higher” in the hierarchy are really met. In this case, the scope of management ought to be changed or a certain preparatory management ought to implement the conditions required. The knowledge of all these relationships increases the chance of investing scarce resources with higher effects on persistence.

Lesson 4 (Chapters 4 to 6):

All the Lessons about the effects of the landscape structure assembled in Section 10.4.1.3 can be interpreted as *Rules of Thumb* for conservational landscape management. They condense important spatial effects on metapopulation persistence in a verbal way and concern aspects such as minimum and optimum conditions for metapopulation persistence, the role of spatial heterogeneity, the choice of an appropriate modelling approach for the persistence analyses etc.. Evidently, these rules are not universal, i.e. valid for all species. They are only valid for *classes of species* sharing a common ecological profile, i.e. a set of ecological attributes which characterize the species' sensitivity to changes in the landscape structure (e.g. strength of environmental noise in the local populations, species' dispersal strategy (dispersal range, generation of a competition effect between the patches for dispersers)). In this sense, the presented rules of thumb are ecologically differentiated.

Lesson 5 (Chapters 4 to 6):

The four tools for decision-support presented (Lessons 1 to 4) condense structural information that gives rise to conclusions about *sources of ecological uncertainty*:
The *approximation formula* T_m^a indicates which species-ecological attributes merely influence the absolute but not the relative results about metapopulation persistence: all attributes which exclusively serve as factor of proportionality in formula T_m^a.
The *Principle of Optimality* reveals that the species' dispersal strategy is a key factor for the optimum patch size distribution. Hence, uncertainty in the species' dispersal strategy matters - but only if there is uncertainty in the following two aspects: whether a competition effect between the patches for dispersers is induced and what landscape elements attract the dispersers (cf. Lesson 4 in Section 10.4.1.5).
The *Hierarchy of Importance* indicates that, as long as a factor on a certain hierarchical level fails the persistence condition required, there is no chance of obtaining long-term metapopulation persistence through changes in factors on lower hierarchical levels. Hence, uncertainty in all the factors on these lower levels does not

influence the absolute results concerning the persistence of a metapopulation.

The *Rules of Thumb* are formulated for classes of species with common ecological profile. Hence, as long as uncertainty in the species' ecological attributes remains within the limits of the profile, the conclusions about the effects of the landscape structure remain unchanged. Uncertainty only matters if it goes beyond the limits.

The presented model-based tools for decision-support have one *major advantage* over the use of software: The decision-maker is no longer dependent on the availability of appropriate software. Once approximation formula, Principle of Optimality, Hierarchy of Importance, or the various Rules of Thumb are published, they can immediately be used by the decision-maker. However, these tools also have a *disadvantage*: They merely support specific aspects of decision-making in metapopulation management. The approximation formula merely supports analyses from the perspective of a particular target quantity (here: the mean lifetime T_m). The Principle of Optimality merely supports the determination of the optimum patch size distribution. Approximation formula and Principle of Optimality are quantitative tools, whereas the Hierarchy of Importance and the Rules of Thumb are exclusively qualitative and providing a rough orientation only. In all cases, a mechanistic understanding of the interplay between landscape structure and species' ecology and its effect on metapopulation persistence was central for the derivation.

10.4.3 Conclusions about metapopulation modeling

One particular challenge in connection with metapopulation modeling is the management of the effects of spatial heterogeneity. The results in Chapter 3 indicate one possible way of model simplification and of combining structural realism with tractability.

Lesson 1 (Chapter 3):

The non-spatial version of the spatially realistic metapopulation model used in this thesis was found to cover all the effects of spatial heterogeneity that are relevant for metapopulation persistence and described by the original model - provided its parameters p are appropriately specified ($p = p_{agg}$). Hence, the entire effect of spatial complexity is summarized in special aggregations p_{agg} of the patch-specific parameters p_i of the original model. This finding is valid for both deterministic and stochastic metapopulation persistence. The rules for the aggregation of the patch-specific parameters p_i, however, differ in the deterministic and stochastic cases.

Lesson 2 (Chapter 3):

The idea to use appropriately aggregated parameters p_{agg} for covering effects of spatial heterogeneity is analogous to the *mean field techniques* widely used in Physics. However, the aggregation rules used in the metapopulation context are more sophisticated than usual arithmetic, geometric, or harmonic means. The aggregation rule E_{agg} for the number of emigrants E_i (see (3.14)), for instance, indicates that E_{agg} consists of special weighted means $\sum_{j(\neq i)} w_j^i \cdot E_j$ of the E_j's where the weights $w_j^i = \frac{a_{ji}}{\sum_{n(\neq i)} a_{ni}}$ depend on the arrival probabilities a_{ki}. This shows that the *aggregation rules reflect the interactions* between the different spatial factors and processes.

Lesson 3 (Chapters 3 and 7):

The fact that a homogenous model in combination with appropriately aggregated parameters covers the effects of spatial heterogeneity is an indicator for complete mixing in the metapopulation. At first sight, this looks surprising because individual dispersal was assumed to be restricted to a certain spatial scale. But note that the dispersing individuals act as “moving reproducing units”: They create new local populations which will be the source for further interactions. In this sense, a single individual can cause a whole sequence of interactions on a much larger spatial scale. In the result, the metapopulation becomes *effectively mixed* in the course of time, although the range of interaction of the single individuals is restricted. The only precondition is that the sequence of interactions does not break down too early. This implies that the colonization rates significantly exceed the extinction rates. This condition, however, has anyway to be met to ensure quasi-stationarity.

10.4.4 Beyond metapopulation persistence

Part III (Chapters 7 to 9) of the thesis aimed at making the experience gained in the course of the metapopulation studies in Part II (Chapters 3 to 6) applicable to other fields of environmental research. We departed from the analysis of (single species) metapopulation persistence and shifted the focus of attention to the following fields of extension:

Original focus (Parts I & II)	*Fields of extension (Part III)*
Single species	Classes of species
Metapopulations	Spatially structured populations
Measures of persistence T_m, λ_M	Other (meta)population dynamical quantities Q
Patchy landscapes	Complex landscapes
Changes in landscape structure	Other critical impacts on biodiversity

Emphasis was placed on drawing methodological conclusions about the use of models for generalization and unification under biocomplexity (Chapter 7) and on deriving ecologically differentiated rules of thumb (Chapter 8) and (meta)population dynamical landscape indices (Chapter 9). The latter two objects provide powerful tools for decision-support in conservational landscape management (note that the approximation formula T_m^a for the mean lifetime derived in Chapter 3 is a special metapopulation dynamical landscape index). In both cases, however, a systematic methodology of their derivation was missing.

The following results address both (a) methodological aspects and (b) some implications of the results attainable from the approaches, methods and protocols presented.

10.4.4.1 Using models for generalization and unification under biocomplexity

In the following, we assemble methods which have been found to be appropriate for supporting generalization and unification under biocomplexity. They concern (a) model building (with special emphasis on bridging the gap between structural realism and tractability), and (b) model analysis (with special emphasis on deriving generalizable results).

We focus on *structural model results* such as typical functional relationships, trends or trade-offs, threshold or optimum values, the relative importance of certain factors, or the functioning of a certain mechanism. To *generalize* a certain result means to test its robustness against changes in the values or submodels for the model parameters, changes in the level of detail, changes in central model assumptions or even in the modeling approach. To *unify* means to deal with the diversity of approaches (not to reduce it!), i.e. to clarify the consequences of choosing a particular approach, to reveal interrelations between the different approaches, and to find bridges between them.

Lesson 1 (Chapter 2 and 7):

Processes on different organismic levels can influence the dynamics of ecological systems. One way of managing the complexity caused by the multi-level structure is *hierarchical model building.* This means that, in a first step, merely the dynamics on the highest organismic level are described by using a generic main model. In the second step, all the relevant effects of lower organismic levels are integrated by the mean of submodels. This strategy of "first subdividing, then integrating" allows structural realism and tractability to be combined without any loss of information, provided feedbacks between the different organismic levels are missing.

Lesson 2 (Chapters 3, 6, and 7):

One way of managing the complexity caused by biological variability is the *search for effective parameters.* The idea is to make use of an ideal, non-structured model and to parameterize it in such a way that aspects of the dynamics of the original model are correctly reproduced. Once appropriately specified, the parameters of the non-structured model summarize all the relevant effects of biological variability covered by the original model. In this sense, these parameters are "effective".

The strategy of searching for effective parameters has several implications. Firstly, it enables a *separate analysis* of all the effects caused by the interplay between the different processes included (covered by the homogeneous model) and all the effects caused by biological variability (covered by the effective parameters). Secondly, to use effective parameters provides a *bridge to important classical models* of population theory the behavior of which is widely investigated and well understood. To take a classical model as a reference is beneficial in two respects: (a) for obtaining a better understanding of more structured models, and (b) for analyzing the functioning of important principles of population theory in more realistic situations. Note that the strategy is only adequate as long as the ecological system is effectively mixed.

There are several approaches of determining effective parameters: (a) diffusion approximation, (b) eigenvalue pertubation, or (c) parameter aggregation.

Lesson 3 (Chapters 3, 4, and 7):

Hierarchical model analysis is a promising strategy in case of hierarchical model systems, that works as follows: In the first step, the model under consideration will be artificially simplified - by neglecting details, assuming homogeneity, or even excluding factors which are known to be decisive. The only aim of this step is to obtain a model which is such simple that it can be analytically solved or its dynamic behavior can be comprehensively studied by systematic parameter variation. This model will then serve as a *reference* for the further analysis. In the second step, all the formerly excluded factors will be consecutively incorporated. By contrasting the results of consecutive model versions, insight will be provided into the effect of the factor currently added and its interplay with the factors incorporated so far. The consecutive increase in the model complexity therefore goes along with a *consecutive generation of knowledge* about the dynamic behavior of the original model.

Lesson 4 (Chapters 5 to 7):

To test the robustness of model results against changes in the model parameters usually requires extensive numerical work in form of parameter variation. Nevertheless, there are several possibilities to *combine numerical work with algebraic analyses.* Algebraic analyses have the advantage that they provide insight into important structural properties and their robustness, without requiring numerical work.

The precondition for algebraic analyses is certain knowledge of the functional structure of the relevant target quantity Q. Hence, algebraic analyses are useful if (a) an approximation formula for the target quantity Q exists, (b) there are equation-based submodels for the model parameters, or (c) the model is related to a classical model of (meta)population theory. The classical models are usually non-structured, analytically solvable and provide structural insight into important effects of the interplay between the relevant processes. This information can be fruitful for the analysis of the original, structured model: It can help to generate *hypotheses* which are worth to be tested and give *hints for the numerical analysis* of the original model.

Lesson 5 (Chapters 6 and 7):

> One particular problem of the recent ecological research, however, is the multitude of models and even modeling approaches which are in use to answer a certain ecological question. Therefore, unification work is needed in the sense of *clarifying the consequences of choosing a particular model or modeling approach.* This requires (a) to compare alternative models regarding their assumptions, definitions of central concepts (e.g. metapopulation persistence), and the target quantities Q considered, (b) to search for common effects and differences, and (c) to classify the conditions under which the models lead to the same conclusions and under which not.

10.4.4.2 Model-based ecologically differentiated rules of thumb

The following results address (a) methodological aspects of the derivation of ecologically differentiated rules of thumb (with emphasis emphasis on chances, limitations, and the development of a rough protocol), and (b) implications of the resulting rules of thumb for ecological research and various aspects of conservation management.

Rules of thumb merely aim at providing a rough orientation for conservation management. This means that they exclusively focus on qualitative key effects which are valid for a wide range of ecological situations. Consequently, they neither support any quantitative assessments nor do they give detailed guidance for any specific situation.

Rules of thumb in general are usually derived in order to strengthen the ecological knowledge basis of conservation management and to support planning and decision processes in this context. Ecologically differentiated rules of thumb for conservational landscape management in particular condense important information about the interplay between a certain (meta)population dynamical target quantity Q of interest and the landscape structure and the role of the species' ecology in this context. They are always of the form "If the species is of type X, then the landscape ought to be of type Y".

Lesson 1 (Chapter 8):

> As the *rough protocol* in Section 8.1.1 indicates, the derivation of ecologically differentiated rules of thumb requires (a) the specification of the management question

to be supported, (b) an appropriate target quantity Q for measuring the effect of management, and (c) an appropriate generic model that takes landscape structure and species' ecology into account and has the target quantity Q as outcome. Central components of the actual model analysis are (1) the determination/analysis of the functional relationship between the target quantity Q and the landscape structure, (2) tests of sensitivity/robustness against changes in the species' ecology and, on this basis, (3) a classification of the species' ecological attributes.

Lesson 2 (Chapter 8):

The strategy of deriving rules of thumb has *limitations of applicability* caused by (a) the presented protocol, or (b) the concept of rules of thumb itself.

The presented protocol assumes that, throughout a simulation run, the landscape structure (habitat quality, patch configuration) is constant. Hence, there is a limitation if the landscape structure becomes *highly dynamic* as is the case if disturbances (e.g. floods, fire, land use regimes) or succession processes are important or habitat quality changes in the course of time. In these cases, however, the protocol can be correspondingly modified. Instead of considering the functional relationship between the target quantity Q and the landscape structure, the relationship between Q and the characteristics of the landscape dynamics ought to be analyzed.

There are limitations of the concept of rules of thumb itself. There are situations where simple rules of thumb cannot be found anymore. The more complex the landscape structure, the lower the chance of finding rules of thumb. This would explain why numerous rules of thumb exist for metapopulations (spatial structure is given by a habitat network that is described by few patch variables (e.g., location, size, shape)) while, for more complex landscape structures, such rules are widely missing.

Lesson 3 (Chapters 4, 5, 6, 8):

Ecologically differentiated rules of thumb have serious implications for *ecological research*. They indicate that we have to think in terms of *classes of species* if we want to understand the effects of the landscape on (meta)population viability or we plan measures of conservational landscape management. Each class is determined by a certain ecological profile, i.e. a set of ecological attributes characterizing the species' sensitivity to changes in the landscape structure. Ecological profiles are used in various contexts to characterize the species' sensitivity to critical impacts: e.g. in *road ecology* (sensitivity to roads) or *ecotoxicology* (sensitivity to pesticides).

Lesson 4 (Chapters 4, 5, 6, 8):

Ecologically differentiated rules of thumb support several aspects of *conservational landscape management*: (a) landscape planning, (b) the development of economic instruments, and (c) the work with stakeholders (integrated assessment).

Landscape planning.– The rules indicate the need to think in terms of classes of species, clarify under which conditions a certain management measure is useful and worth to be considered at all, and help the planner to determine which management measures out off a variety of alternatives is most efficient.

Development of economic instruments.– The rules support the development of effective and efficient economic instruments for conservational management. They provide conditions for ecological effectiveness and efficiency. Last but not least, they give rise to the conclusion that the utility function, the heart of any cost-benefit analysis, has to take both the landscape structure and the species' ecology into account if it is used in the context of conservational landscape management.

Integrated assessment.– Conservation management is multi-criteria and multi-agent. Hence, stakeholder involvement and learning processes become increasingly important. Both are supported by rules of thumb which condense information about the relationship between species' survival and landscape structure in a verbal way. Hence, they help to clarify the consequences of a considered scenario and to differentiate between alternatives. This strengthens the scientific basis and the transparency of the decision process and increases the chance of more sustainable decisions.

10.4.4.3 Model-based (meta)population dynamical landscape indices

The following results address (a) the development of a systematic approach and a rough protocol for the derivation of (meta)population dynamical landscape indices, and (b) implications of such indices for landscape analysis and conservational landscape management, but also for ecological research and the methodology of integrative modeling.

The idea of (meta)population dynamical landscape indices is analogous to that underlying the approximation formula T_m^a for the mean lifetime of metapopulations: The aim is to describe the functional relationship between the (meta)population dynamical target quantity Q of interest and the landscape structure by a simple formula (the index).

The study surveyed eight (meta)population dynamical indices. Evidently, there is a high diversity of methods used for their derivation. The spectrum reaches from regression analysis and spatial statistics to algebraic analysis and eigenvalue approximation. The study aimed at systematizing the different methods and concluding a rough protocol.

Lesson 1 (Chapter 9):

> The functional relationship between any (meta)population dynamical target quantity Q and the landscape structure can only be fully understood if the interplay between the individuals and the landscape structure is taken into account. Whether this interplay is explicitly described or implicitly included via its effect on relevant processes markedly influences the complexity and so the methods for exploring the relationship between Q and the landscape structure. This led to the following *classification of spatial (meta)population models* which can be used as starting point for index derivations: (a) individual-based spatially explicit models, (b) individual-based metapopulation models, and (c) presence-absence metapopulation models. These three classes cover a wide range of spatial (meta)population models.
> In the cases (a) and (b), the interplay between the individuals' and the landscape structure is explicitly described, whereas, in case (c), the interplay is implicitly included. In case (a), the landscape structure can be complex, whereas, in the cases (b) and (c), a simple landscape structure (configuration of patches) is assumed.

Lesson 2 (Chapter 9):

> For each of the three model classes, a *rough protocol* for the derivation of (meta)-population dynamical landscape indices has been developed (Section 9.2). The major difference between the individual protocols is that, in the case of individual-based spatially explicit models, there is a need to determine a set of landscape variables

v_s which are decisive for the functional relationship between Q and the landscape structure. In the two classes of metapopulation models, the decisive landscape variables v_s are already known from the beginning. This reduces the complexity. With decreasing complexity (a $\triangleright$ b $\triangleright$ c), there is a clear gradient from statistical to partly analytical/algebraic methods for describing the relationship between Q and the v_ss. All the existing methods of index derivation fit in the overall scheme.

Lesson 3 (Chapter 9):

In all three cases, the resulting (meta)population dynamical landscape indices Q^I have the same functional structure: $Q^I = F_{\mu,\nu..}(v_s)$ where the v_ss are the decisive landscape variables, $F_{\mu,\nu..}()$ a certain function and $\{\mu, \nu..\}$ certain function parameters. The landscape variables v_ss summarize all the spatial effects on the target quantity Q, whereas $F_{\mu,\nu..}()$ summarizes all the effects of the species' ecology. Hence, $F_{\mu,\nu..}()$ can be interpreted as "species-specific glasses" through which the landscape can be analyzed and interpreted in terms of its (meta)population dynamical effect.

Lesson 4 (Chapter 9):

The concept of "(meta)population dynamical landscape indices" $Q^I = F_{\mu,\nu,..}(v_s)$ goes beyond the concept of *"ecologically scaled landscape indices"* in the sense of Vos et al. (2001) whose idea was to link landscape structures to ecological processes by appropriately scaling, i.e. relating the relevant landscape variables (e.g. area, distance) to the spatial scale on which the modeled organisms typically act. $F_{\mu,\nu,..}()$, however, indicates which species-specific characteristics (namely $\{\mu, \nu, ..\}$) are actually needed for adequately reflecting the combined species-landscape effect on Q. This can be critical spatial or temporal scales, but also other characteristics (e.g. strength of environmental noise in the local populations). In this sense, the $F_{\mu,\nu,..}()$-approach is wider, more flexible and better adapted to ecological processes than a pure scaling-approach. It provides a bridge between *neutral landscape models* (commonly used in landscape ecology) and spatial (meta)population dynamics.

Lesson 5 (Chapter 9):

If two species coincide in the species-specific glasses $F_{\mu,\nu,..}()$ then they also coincide in the landscape index $Q^I = F_{\mu,\nu,..}(v_s)$. Hence, the two species show the same sensitivity to changes in the landscape structure, as far as the effect on the target quantity Q is concerned. This indicates that $F_{\mu,\nu,..}()$ can be used as a basis for an ecological classification of the species according to their demands on the landscape management. This is the same sort of classification as was used in connection with the derivation of ecologically differentiated rules of thumb for landscape management. Hence, (meta)population dynamical landscape indices $Q^I = F_{\mu,\nu,..}(v_s)$ and ecologically differentiated rules of thumb are closely linked to each other. Both together provide a *powerful toolbox* for the *analysis and management* of ecological *classes of species*. While the rules give a rough qualitative orientation for the management (e.g. for prioritizing), the indices enable quantitative assessments of the effect of landscape changes on the (meta)population dynamical target quantity Q.

Lesson 6 (Chapter 9):

(Meta)population dynamical landscape indices $Q^I = F_{\mu,\nu,..}(v_s)$ are *surrogates* of spatial (meta)population models. They condense important information about the interplay between individuals and landscape structure and its effect on the target quantity Q in form of *input-output relations*. Such relations can be (a) integrated in more complex studies (e.g. integration of the index for the arrival probability a_{ij} in metapopulation models), (b) used as objective functions in optimization algorithms for reserve network design, or (c) used as starting point for the development of utility functions $U(Q) = U(F_{\mu,\nu,..}(v_s))$ which allow landscape structure and species' ecology to be integrated in cost-benefit analyses in the context of conservational landscape management. This indicates that (meta)population dynamical landscape indices $Q^I = F_{\mu,\nu,..}(v_s)$ open *new possibilities of integrative modeling*: To integrate the indices is a powerful alternative to integrating the underlying models.

Although we started with the subject of metapopulation persistence, we could draw conclusions which go beyond this subject and support further fields of environmental research.

10.5 Concluding remarks

The overall thesis gives rise to some general remarks on the possibilities to contribute to a methodology of using models for theory building and management support in environmental research and on the chances and limitations of the problem-oriented approach. In the context of metapopulation persistence, a number of methods for supporting generalization and unification and for deriving model-based tools for decision-support have been derived. These methods could be extended to other fields of environmental research. A closer look at these methods, however, reveals that the *range of extension is limited*:

1. The presented methods for supporting generalization and unification primarily aim at reconciling closeness to biological realism and tractability. This requires management of biocomplexity. In the context of metapopulation persistence, three sources of biocomplexity could be distinguished: (a) diversity of organismic levels involved, (b) diversity of processes interacting on a particular level, (c) biological variability. The methods presented allow particular sources of complexity to be managed, e.g.

   hierarchical model building and analysis ⟶ diversity of organismic levels
   work with effective parameters ⟶ biological variability.

   Hence, these methods are merely applicable/extendable to situations which are characterized by the *same sources of biocomplexity* as metapopulation persistence.

2. The presented methods for deriving model-based tools for decision-support are extendable in two respects but to a limited range of situations as well. Firstly, the methods share a common starting point: systematic analyses of the interplay between *landscape structure, species' ecology and stochasticity* and its effect (note that this interplay is central in the context of metapopulation persistence). Hence, the methods are applicable/extendable to situations for which this *interplay is central as well*. Thus, extension is merely possible within the components involved in the interplay. In spite of this restriction, important extensions are possible (→ complex landscapes, → classes of species, → other ecological target quantities). Secondly, the presented methods enrich disciplines which *use ecological information as input* (e.g. development of economic instruments, integrative modeling).

All these arguments show that the structural characteristics of an environmental problem (e.g. sources of complexity, essential factors and their interplay) determine the range of extendability of methods originally developed for model-based theory building and management support in the context of the particular environmental problem considered.

To differentiate between different sources of complexity is found to be promising. This allows the development of methods which are specifically geared to the specific nature of each source of complexity. In this way, complexity can be managed more effectively.

The thesis provided insight into chances and limitations of theory building and management support under biocomplexity. The experience gained in the course of this work can be used as a starting point for the *next step* that is theory building and management support under *biocomplexity and interdisciplinarity.* This is especially relevant if environmental problems are addressed which occur at the edge between ecology and economy. To contribute to a methodology is one objective of my future research.

Chapter 11

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