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# Metapopulations, Markets and the Individual

## Refining incentive-based approaches for biodiversity conservation on private lands

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# Metapopulations, Markets and the Individual

## Refining incentive-based approaches for biodiversity conservation on private lands

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## Metapopulations, Markets and the Individual - Refining incentive-based approaches for biodiversity conservation on private lands

**Abstract:** *When designing financial incentives for voluntary conservation of threatened habitats and ecosystems, we are faced with the problem that there is no single indicator for "biodiversity value". The value of a habitat depends on multiple factors such as habitat type, area, and spatial and temporal connectivity. Moreover, not only are there local trade-offs between these indicators, but land use changes at one location may also change the value of sites in the vicinity. This doctoral thesis analyzes the consequences of including trade-offs and interactions between sites in market-based conservation schemes. We ask the following questions: How can trade-offs between the survival of different species be quantified? How can spatial processes and temporal processes be included in market-based conservation, in particular the value of spatial and temporal connectivity? And how do underlying economic dynamics relate to the spatio-temporal allocation of conservation measures in market-based conservation schemes?*

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# Preface

During the last millennia, humans have become the most successful species ever to inhabit our planet, considering their dominance in nearly all geographical and climatic zones, their ability to shape their habitat, and their potential to outcompete other species. Yet, whether they will be able to sustain this dominance at evolutionary timescales remains to be proven. In the course of the Earth's history, human evolution has barely lasted a blink of an eye, and chances for failure are manifold. The breathtaking evolution of human culture, including knowledge and technology, has led to a rapid increase of resource consumption and a steady and unhalted growth of the human population.

While the signs of increased human activity are evident, its long-term effects are still uncertain. The biosphere has been subject to massive anthropogenic changes, and ecosystems are far from having reached a stable equilibrium again. The emission of carbon dioxide and other greenhouse gases has made substantial changes to the atmosphere, resulting in an ongoing increase of the earth's surface temperature and a change of local climate and precipitation patterns. As a consequence, ecosystems and the services they provide to humans are changing. Biodiversity, which contributes to the provision of direct and indirect ecosystem services, is declining at an alarming rate. This loss is likely to cause negative impacts on human well-being, including decreasing food, water and energy security and an increase of vulnerability to natural disasters.

And yet, although the danger of an unhalted depletion of the Earth's resources are ever so apparent, nations find themselves struggling to identify appropriate measures to reverse this trend. The time lags of global changes may be several decades, meaning that nowadays, we only experience the effects of the lifestyle of our preceding generation, while the consequences of our current lifestyle will affect the generations to come. The human population is still growing, projected to reach nine billion people in 2050. But even more concerning and consequential than population growth is the current growth of economic productivity, driven by the desire of emerging economies to reach the lifestyle of industrialized societies as much as by the industrialized countries which have embraced economic growth and consumption as the supplier of prosperity, individual freedom and social reconciliation.

Therefore, science and decision makers are challenged to create robust institutional settings for controlling global land use and resource consumption. In recent years, market-based instruments have become increasingly popular to change economic incentives of actors, with the goal of inducing more sustainable land use patterns. But how can we create markets for things which are as diverse and heterogeneous as our ecosystems? What is the right measure, and the appropriate scale, for creating financial incentives for the conservation of biodiversity? In this dissertation, we examine the effectiveness of different incentive systems for voluntary conservation measures on private lands, with a particular focus on creating incentive systems that account for the spatial and temporal processes which govern natural population dynamics.

# Contents

Chapter 1

# Introduction

## 1.1 Evidence and drivers of biodiversity loss

Somewhat ambiguous in its definition, biological diversity or biodiversity is usually defined as "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" (UNEP, 1992). Thus, biodiversity encompasses not only genetic diversity, but also the diversity of functions and responses that are associated with the world's ecosystems. While many claims and theories around biodiversity have been challenged, two facts cannot be questioned: The world's ecosystems are losing biodiversity at unprecedented speed (Fig. 1.1), and the main causes of this loss are anthropogenic. The subsequent loss of valuable ecosystem functions and services such as food production, water filtration, crop pollination or climate regulation is only one reason for growing concern (Loreau et al., 2001; Balmford et al., 2002). Another potential effect is that the loss of diversity increases the vulnerability of ecosystems to disturbances induced by climate change, invasive species or new diseases (McCann, 2000; Chapin III et al., 2000; Folke et al., 2004; Hooper et al., 2005).

The reasons for the ongoing loss of biodiversity are manifold, and complex. Yet, the growth of the human population in the last centuries, accompanied by an increase in productive capacity, resource consumption and mobility per capita are undoubtedly the primary drivers that are causing the observed effects (MA, 2005). They directly relate to habitat loss, to overharvesting of natural stocks, to prevalence of pollutants and toxic substances and to the introduction of invasive species through human transport. Additionally, ecosystems have to cope with secondary effects such as climate change, a reaction of the combined system of atmosphere, biosphere and hydrosphere on the increased emission of greenhouse gases that results in an ongoing increase of global temperature and a change of local climate and precipitation patterns.

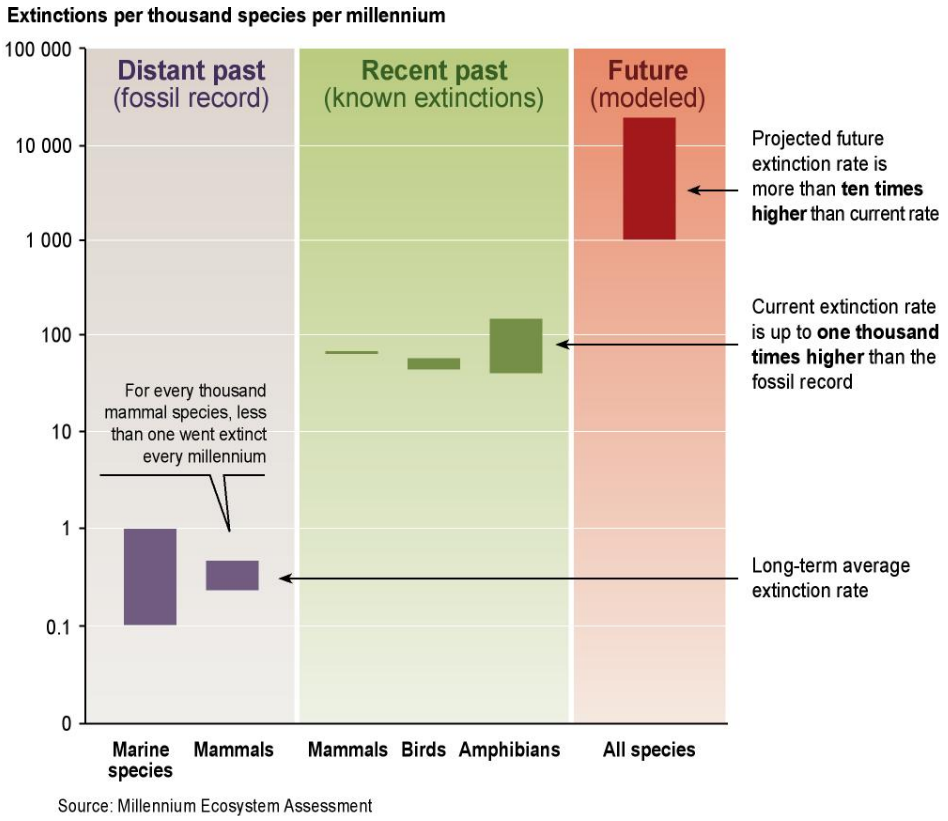
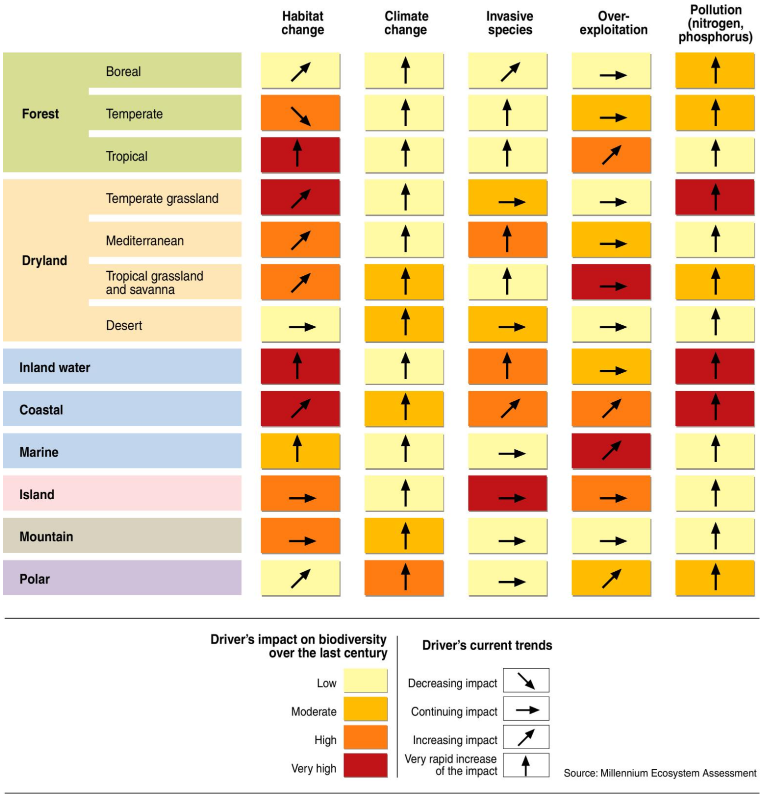


**Figure 1.1:** Biodiversity loss: Past, present and future extinction reates. Recent extinction rates are about 100 to 1000 fold higher than extinction rates that are found in fossil records. Source: Millennium Ecosystem Assessment (MA, 2005)

Although the mechanisms of biodiversity loss are fairly well understood, there is little evidence for a successful mitigation or reverse of this trend for any driver or ecosystem (Fig. 1.2). The human population is still growing, projected to reach 9 billion people by 2050. But equally concerning and consequential as population growth is the growth of economic productivity. The growth of wealth per capita in developed and emerging countries has led to an ongoing increase in resource consumption, which has absorbed most positive effects of cleaner technologies and environmental regulations. Thus, a majority of studies estimates that the pressure on ecosystems around the world is likely to grow in the future, in particular when current pressures are combined with the projected effects of climate change (Tilman et al., 2001).

One of the reasons for the prevalence of these trends is the lack of institutions that may successfully control the use of resources on our planet. For many shared resources, *individual benefits* of resource overuse are larger than the *individual costs*. From the perspective of a travelling individual for example, the benefits from using a plane are greater and more immediate than the consequences from climate change, which are shared among



| | | Habitat change | Climate change | Invasive species | Over-exploitation | Pollution (nitrogen, phosphorus) |
|---|---|---|---|---|---|---|
| Forest | Boreal | Low ↗ | Low ↑ | Low ↗ | Low → | Moderate ↑ |
| | Temperate | High ↘ | Low ↑ | Low ↑ | Moderate → | Moderate ↑ |
| | Tropical | Very high ↑ | Low ↑ | Low ↑ | High ↗ | Low ↑ |
| Dryland | Temperate grassland | Very high ↗ | Low ↑ | Moderate → | Low → | Very high ↑ |
| | Mediterranean | High ↗ | Low ↑ | High ↑ | Moderate → | Low ↑ |
| | Tropical grassland and savanna | High ↗ | Moderate ↑ | Low ↑ | Very high → | Moderate ↑ |
| | Desert | Low → | Moderate ↑ | Moderate → | Low → | Low ↑ |
| Inland water | | Very high ↑ | Low ↑ | High ↑ | Moderate → | Very high ↑ |
| Coastal | | Very high ↗ | Moderate ↑ | High ↗ | High ↗ | Very high ↑ |
| Marine | | Moderate ↑ | Low ↑ | Low → | Very high ↗ | Low ↑ |
| Island | | High → | Low ↑ | Very high → | High → | Low ↑ |
| Mountain | | High → | Moderate ↑ | Low → | Low → | Low ↑ |
| Polar | | Low ↗ | High ↑ | Low → | Moderate ↗ | Moderate ↑ |

Driver's impact on biodiversity over the last century: Low, Moderate, High, Very high

Driver's current trends: Decreasing impact ↘, Continuing impact →, Increasing impact ↗, Very rapid increase of the impact ↑

Source: Millennium Ecosystem Assessment

**Figure 1.2:** Drivers of biodiversity change and their trend for the future. Source: Millennium Ecosystem Assessment (MA, 2005).

all humans and which will only appear in the future. Yet, when accounting for *societal costs*, there is considerable evidence that the total costs of these actions exceed their benefits by far (Costanza et al., 1997). Nevertheless, because some actors benefit from resource overuse, individuals, states and even parts of the world are overusing environmental resources, creating a negative net effect on the wealth of the planet, which results in a welfare loss for current and future generations. This phenomenon, namely that individual actors deteriorate a shared resource because they can pass on the costs to others, has become known as the *tragedy of the commons* (Hardin, 1968).

## 1.2 Current policy response

Building institutions that correct incentives to overuse shared resources is one of the big challenges for developing sustainable economies. How do we limit the use of formerly unrestricted resources, while at the same time providing sufficient freedom and equity to individuals, communities and nations, enabling them to shape their life in the way they intend? For the case of $CO_2$ emissions, many states have agreed on a tradable permit system, giving each country a number of permits that act as an emission allowances (Tietenberg, 2006). Each country agrees to limit its emission to the issued permits. Parties that decrease their emissions below their permitted quantity may sell those permits to other parties, limiting global $CO_2$ emissions while leaving emitting parties with the possibility to bargain over the price and the allocation of emissions.

For the problem of sustainable land use and biodiversity conservation, *command and control* approaches have largely dominated in the past. Land is assigned to certain land use types such as conservation, agriculture or housing, with use restrictions applying to each of these types. Land use planning has had some success in mitigating environmental problems, such as controlling urban sprawl and limiting the destruction of threatened habitats. Yet, it has become apparent in recent years that current planning efforts will not suffice to halt the ongoing biodiversity loss across the world's ecosystems. One reason is that conservation planning is very costly, limiting the amount of land that can be set aside for conservation. Another reason is that centrally planned conservation faces considerable resistance when conflicting with economic or private interests of stakeholders.

Therefore, there has recently been increasing interest in *market-based approaches* to conservation such as *payment schemes* or *tradable permits* (Salzman, 2005; Wissel and Wätzold, 2008; Jack et al., 2008). Similarly to carbon emissions trading systems, market-based conservation policies aim at creating financial incentives for land owners to voluntarily engage in biodiversity conservation on their land. Examples of market-based instruments are *payments* (Wunder, 2007; Drechsler et al., 2007), *auctions* (Latacz-Lohmann and Van der Hamsvoort, 1998) or *biodiversity offset trading* (Panayotou, 1994; Chomitz, 2004). One advantage of conservation markets is the higher acceptance for these policies because private landowners are not forced to certain actions, but voluntarily join a conservation scheme when it seems profitable to them. Another advantage is that competition between landowners ideally results in conservation being undertaken by those with the lowest costs, creating potentials for cost savings and enabling authorities to sustain larger conservation schemes as could be financed with planning approaches.

Still, there is a number of open questions associated with market-based conservation. Among them, one of the most important problems is how to define the "amount of conservation" provided by different conservation actions. Unlike carbon markets, which simply trade the amount of carbon emitted, habitats are highly diverse, they are subject to successional dynamics, and their functional value depends strongly on the spatio-temporal characteristics of the surrounding lands. To make habitats tradable, we need to define rules that translate the diversity of possible types and functions into one "currency". This process of mapping formerly non-marketed and therefore non-comparable goods or services into one currency is often referred to as commodification or commoditization (Salzman and Ruhl, 2000). Once a conservation is established as a commodity, i.e. as a good that can be measured with a single value, we may create incentives for conservation, for example by offering a certain price per unit of the commodificated conservation actions.

Besides the large heterogeneity of ecosystem types and functions, one of the biggest challenges for creating appropriate incentive systems is that many ecological processes operate at much larger spatial and temporal scales as could be controlled by an individual landowner: Populations interact over large distances, they may have very particular habitat requirements, or there may be time lags between impacts and ecological effects. Therefore, unlike carbon markets, where the amount of carbon saved has the same effect regardless from where and when this is done, biodiversity measures are highly dependent on their spatial and temporal allocation.

## 1.3 Research questions

The aim of this doctoral thesis is to find effective incentive mechanisms for market-based instruments. These incentive mechanisms should include sufficient ecological detail, while at the same time being robust and applicable for real world conservation schemes. A particular focus of the research is to examine how spatial and dynamic ecological processes that lead to spatial and temporal interactions between the values of local sites may be included into incentive mechanisms. Our main questions are:

1. **Trade-offs between species types:** How can trade-offs between conservation measures for different species be quantified?
2. **Inclusion of spatial processes:** How can spatial processes, in particular metapopulation processes and the control of landscape fragmentation, be included in market-based conservation?
3. **Dynamics of markets and ecology:** How do economic drivers affect the dynamical allocation of conservation measures, and how can conservation markets account for temporal processes such as landscape dynamics and time lags of restoration measures?

The following chapter discusses the concepts and methods that were used to answer these questions. Chapter 3 contains the research papers that were published or prepared during this PhD. We conclude with a discussion of our results in chapter 4.

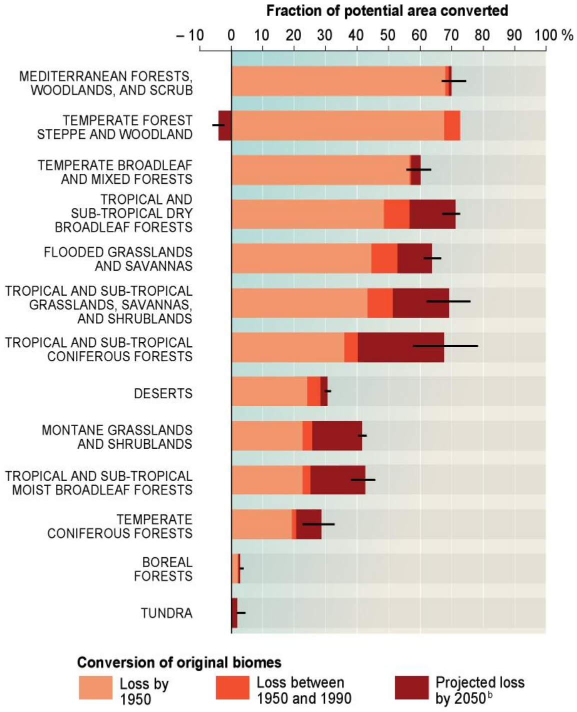
Chapter 2

# Concepts and Methodologies

The aim of this chapter is to summarize the assumptions and methods that are necessary to understand our research results. The first two sections cover ecological assumptions and methods: in the first section 2.1, we summarize the processes that govern and threaten populations at a landscape scale. The modeling approach chosen for quantifying these processes is presented in section 2.2. The following two sections deal with the economic assumptions underlying our research: section 2.3 explains the principles of market-based conservation, and section 2.4 discusses our assumptions about how individual landowners will react to the financial incentives created by market-based conservation policies. The last section 2.5 discusses how to combine these ecological and economic models, and how to compare the ecological and economic success of different policies.

## 2.1 Habitat loss, fragmentation and landscape dynamics

When looking for reasons of the decline of biodiversity within the last centuries, *habitat loss* and *fragmentation* are usually named as two of the main drivers (Andren, 1994; MA, 2005). Fig. 2.1 displays current evidence for habitat loss – in all biogeographical regions of the world, there has been a major decline of natural biotope types, leading not only to a loss of habitat, but also to increasing fragmentation of the remaining areas. Additionally, not only the area and the spatial location, but also the dynamics of habitats have been changed by humans, for example by controlling natural succession or creating new and larger scale disturbances. As mentioned in the introduction, there are more processes which threaten biodiversity, one of the foremost being biotic invasions (Mack et al., 2000). For this thesis, however, we have concentrated on habitat loss, fragmentation and landscape dynamics, because these three processes are most closely linked to the land use that can be controlled by market-based incentive schemes. The following subsections give a summary of our current understanding of why and how these three processes may cause the extinction of species and the loss of biodiversity.



[a] A biome is the largest unit of ecological classification that is convenient to recognize below the entire globe, such as temperate broadleaf forests or montane grasslands. A biome is a widely used ecological categorization, and because considerable ecological data have been reported and modeling undertaken using this categorization, some information in this assessment can only be reported based on biomes. Whenever possible, however, the MA reports information using 10 socioecological systems, such as forest, cultivated, coastal, and marine, because these correspond to the regions of responsibility of different government ministries and because they are the categories used within the Convention on Biological Diversity.

[b] According to the four MA scenarios. For 2050 projections, the average value of the projections under the four scenarios is plotted and the error bars (black lines) represent the range of values from the different scenarios.

Source: Millennium Ecosystem Assessment

**Figure 2.1:** Loss of natural biomes around the globe. Source: Millennium Ecosystem Assessment (MA, 2005).

### 2.1.1 Habitats and populations

A *habitat* is a geographical area that is used by individuals of a species. As Begon et al. (2006) put it, "where an organism lives is its habitat". The term habitat is always specific to a particular species. Different species may have different, often highly specific biotic and abiotic habitat requirements. Examples of such requirements could be the existence of food, water or shelter within a certain distance, as well as particular soil compositions and climatic conditions. Thus, the habitat quality of a particular site may differ largely depending on the species we are concerned with.

The amount of individuals within a particular habitat is limited. Limiting factors are resources, but also intra- or interspecific interactions or externally induced mortality due to catastrophic weather events, floods or fires. As long as these limitations are small, reproduction is usually well approximated by the model of exponential growth (Fig. 2.2 a).

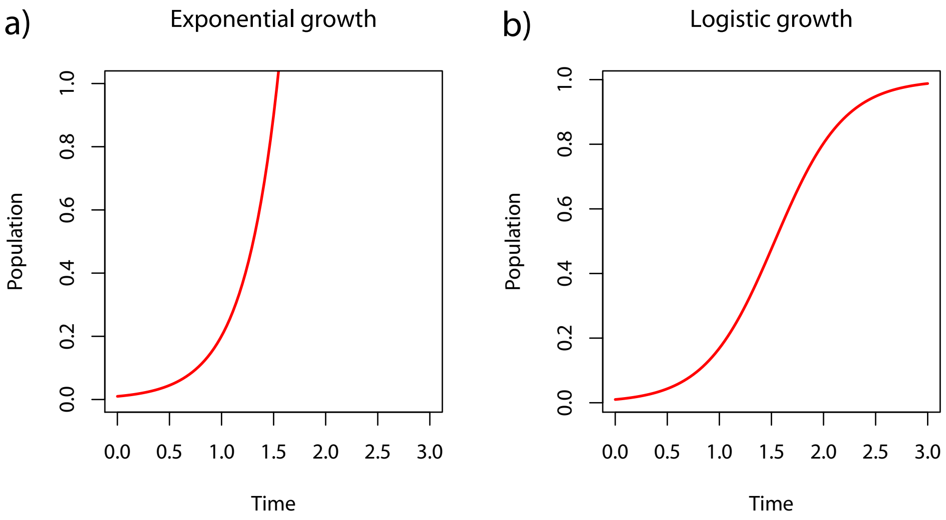


**Figure 2.2:** Exponential (left) and logistic growth (right). Note that logistic growth is approximately exponential at low population density (left part of the curve). At higher population densities, population growth decreases until the population approaches the carrying capacity.

When resources get scarce, the effective population growth is declining. The equilibrium level at which reproduction and mortality rates balance each other is usually referred to as the *carrying capacity*. Fig. 2.2 b shows a graph of the logistic equation, the simplest models to describe how population growth approaches the carrying capacity.

The models of exponential and logistic growth describe the development of a population size as a deterministic process, where a certain population size will always develop with the same trajectory in time. Particularly for small populations, however, stochastic effects may play a decisive role for describing the population development. Examples for this are *demographic stochasticity* (stochastic effects on the population dynamics) or *environmental stochasticity* (fluctuations of environmental conditions). Accounting for stochastic effects is important because this allows for understanding the origin of extinction processes and estimating extinction risks of a species. Smaller populations are more endangered to go extinct because they lack a sufficient number of individuals to buffer demographic and environmental fluctuations. Therefore, habitat loss, leading to decreasing carrying capacities, increases the extinction risk of species.

### 2.1.2 Dispersal and fragmentation

Species are not only threatened by decreasing available habitat area, but also by the *fragmentation* of these areas. The term fragmentation refers to landscapes where habitable areas (patches) are surrounded by areas that are hostile to the species (matrix). As demographic or environmental stochasticity may lead to extinctions of a species on any local site, it is vital for a species that some individuals leave their current habitat and search for unoccupied habitats that can be colonized. The phenomenon of organisms leaving their current habitat, population or parent organism is called *dispersal*. Often, species dispersal is associated with a particular life stage, such as the seed dispersal of plants. For other species, dispersal is triggered by biotic or abiotic conditions, for example by resource scarcity or weather conditions.

Dispersal can be active, i.e. the movement is maintained through the organism itself, or it can be passive, using the environment to disperse. Examples for the latter are dispersal of seeds through wind, or dispersal of parasites through the movement of their host. Dispersal may be directed, meaning that individuals are aware of their environment and try to reach a certain location, or undirected, meaning that the movement is largely random until individuals find a reason to stop their movement. All species use dispersal to distribute themselves or their offspring to new locations. Understanding dispersal and movement behavior is therefore vital to understand how species experience distances and how this relates to their survival probability in spatially structured habitats (Wiens et al., 1993; Tilman, 1994).

With increasing loss of habitable area, landscapes have become increasingly impermeable for species, with a range of negative consequences such as the loss of genetic exchange or the inability to recolonize isolated habitat patches (Saunders et al., 1991; Fahrig, 2002). One of the main aims of conservation is therefore not only to conserve a sufficient amount and diversity of habitats, but also to preserve the structural connectivity of these habitats. Consequently, when fragmentation is a conservation concern, the importance of a local site is not only given by its habitat type and size, but also by its location within a larger region and the species-specific effort which is necessary to travel between the available habitats.

### 2.1.3 Changing landscape dynamics

As habitat loss and fragmentation are perceived as the main drivers of biodiversity loss at the landscape scale, conservation efforts of the last decades have mostly concentrated on halting the loss of rare habitats and biotopes, restoring valuable habitats if possible, creating corridors between habitats and mitigating landscape fragmentation. The rationale behind these efforts has mainly been a static one, trying to find the most valuable site or the best possible conservation measure in the current landscape. It has, however, become apparent that the assumption of static external conditions may in some cases be insufficient to address our current conservation problems (Pressey et al., 2007).

The reason is that both ecosystems and economic systems are subject to changes. Human-dominated, cultural landscapes across the globe have always been dynamic. Traditional farming practices, such as plowing or fallow fields, managed burnings, or the creation of quarries, used to induce landscape dynamics that created niches for a variety of species. Yet, even without these anthropogenic drivers, there are many landscapes whose steady state is inherently dynamic on smaller scales, such as fire-driven forest and savanna systems, precipitation patches in arid regions, upwellings in the marine ecosystems, or disturbed patches in floodplains.

In the last decades, humans have massively changed traditional landscape dynamics. As an example, modern farming practices allow large scale harvesting, leading to country-wide synchronized disturbances, whereas traditional management included continuous harvesting of small patches over a period of several weeks. Wild fires are managed to avoid economic losses and human casualties. Floods are increasingly controlled, enabling the conversion of floodplains to agricultural or urban areas.

The effects of changing landscape dynamics on biodiversity have largely been negative (Hobbs and Huenneke, 1992). The problem of preserving natural dynamics has been acknowledged in the literature (see e.g. Bengtsson et al., 2003; Pressey et al., 2007), however, protection of landscape dynamics, in particular on a large scale, is still a major challenge. Conserving dynamic landscapes requires much larger areas than static conservation, which implies even larger demand for public funds when conservation is organized through land purchase (Bengtsson et al., 2003). Particularly for the problem of creating dynamic landscapes, *market-based approaches* are a promising alternative to traditional, centrally managed conservation policies. Market-based (also called incentive-based) policies can be used to change financial incentives of land users in order to encourage more traditional landscape dynamics on private lands. As an example, several schemes in Europe try to alter the dynamics of agricultural landscapes by legal regulations and subsidies through payments for mowing fields only after a certain date. This example, however, also shows a danger of market-based interventions, which is that incentives may be too coarse and therefore lead to undesired side effects. Konvicka et al. (2008) reports that one of these schemes, which was targeting meadow birds, led to a dramatic decline of a threatened butterfly species, *Colias myrmidone*, from the White Carpathians in the Czech Republic. The reason was that incentives for late mowing led to a country-wide, synchronized disturbance at the earliest possible date that was still financially supported by the scheme. This synchronized disturbance coincided with an important time in the life-history of the butterfly, and presumedly also harmed other species that depend on these meadows. The conclusion here is that, when applying market- based interventions, incentives have to be targeted to ensure that they produce controlled and heterogeneous landscape dynamics, respecting the need of all endangered species and habitat types.

## 2.2 Metapopulation models

There is a number of possible models and model approaches that capture the processes mentioned in the preceding section, among them *individual based models* (Grimm and Railsback, 2005), *metapopulation models* (Hanski, 1998, 1999b), and *reaction diffusion equations* (Holmes et al., 1994). Broadly speaking, metapopulation models are more aggregated than individual based models, and less aggregated than reaction-diffusion models.

In our research, we decided for the use of metapopulation models, because they are well adopted to describe stochastic population dynamics and the effects of fragmentation on the landscape level. Also, they are computationally sufficiently fast to qualify for parameter scans, optimization and statistical analysis of species survival, which was important for our analysis. We used stochastic, time discrete metapopulation models throughout our research. In the rest of this section, we give a short introduction to stochastic metapopulation models and their typical properties. For a discussion of the deterministic and type continuous metapopulations such as the classic Levins model (Levins, 1969), we refer to the literature, e.g Hanski and Gilpin (1991); Hanski (1999b).

### 2.2.1 State variables - a network of patches

The central concept of a metapopulation model is the *patch*. A patch is a spatially distinct area of suitable habitat for the species under consideration. Each patch has a location in space and may be inhabited by populations of one or several species. The local population dynamics of species may be modeled by very simplistic or more complicated models, which will later be discussed in more detail (section 2.2.2). The important point, however, is that within a patch, spatial processes are neglected and the patch is viewed as a homogeneous pool for the species.

#### Patches, matrix and the network

The surrounding of a patch, which is assumed to be hostile or at least not beneficial for the species is called the *matrix*. A number of patches is said to form a *metapopulation network* if the allocation of patches in the matrix is such that there is a non-vanishing probability for individuals to disperse between any of the patches (possibly be means of intermediate patches), but exchange rates between patches are so low that each patch may, in good approximation, be treated as an independent subpopulation with its own population dynamics.

A metapopulation network with patches as nodes and dispersal paths as vertices between those nodes may then be classified by macroscopic network properties such as connectivity measures, number of patches, or average patch area. In a more dynamical view, emerging flows of individuals between the patches may also be used to categorize patches, for example into source patches that are typically sending out more individuals than they receive, and into sink patches for which the opposite is true.

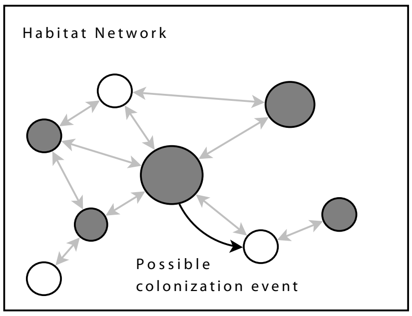


**Figure 2.3:** A metapopulation network: The network is defined through the possible dispersal paths that connect patches with each other (straight arrows). Dark patches are populated, white ones are temporally unpopulated. The bent arrow marks a possible colonization event from a populated to an unpopulated patch.

### Applicability of the patch concept

There are some limitations to the patch concept: patches must be large enough to sustain a local population, and they must be small enough to justify the neglect of spatial processes within the patch. Clearly, small and large here depends on the characteristics of the species, i.e. its typical movement behavior and its population dynamics. Finally, landscapes have to display sufficiently sharp boundaries to allow for the distinction between patch and matrix. Particularly human dominated landscapes are often characterized by sharp boundaries and medium size land use units. Thus, smaller species that operate on a scale of the order of a few hundred meters to a few kilometers qualify well for a description through metapopulation models. For some other species such as large predators or for other landscapes such as marine ecosystems, the partition of the landscape in patch and matrix is less obvious, and therefore other population models such as IBMs or spatially implicit models may be preferable.

## 2.2.2 Processes in spatially structured populations

A fundamental assumption of metapopulation models is that the subpopulations inhabiting single patches are threatened by local extinctions on intermediate timescales. Such extinctions of a local population may originate from demographic stochasticity, environmental stochasticity such as weather conditions, or catastrophes such as the appearance of a pest or a predator. It is therefore unlikely that a subpopulation on a single patch will persist on intermediate timescales. The whole metapopulation, however, can persist, because dispersal from remaining subpopulations may stabilize the network both by recolonizing empty patches and by reducing the extinction probability of existing populations through inflow of new individuals (rescue effect) (Hanski et al., 1996). Still, although stability increases rapidly with the number of patches, there is a remaining probability that too many local populations go extinct at the same time, with the consequence that the whole metapopulation goes extinct. Thus, metapopulation networks are generally in a quasi-stationary state, which typically has a small, but not vanishing extinction probability. We will discuss the functional relation between survival of the metapopulation and variables such as patch number or network connectivity in section 2.2.4. In the rest of this subsection, we give a short introduction to the typical processes included in metapopulation models.

### Local population dynamics and local extinction

In the most simple explicitly stochastic metapopulation models, *local population dynamics* are just binary, i.e. a patch is either populated or not. In this model type, a populated patch is subject to a (possibly time or network dependent) local extinction risk. The justification of this assumption is the separation of timescales between local population dynamics and metapopulation dynamics: If local population dynamics are much faster than metapopulation dynamics, which are coupled to recolonization, local populations will practically instantaneously approach their carrying capacity and then be subject to a constant extinction risk. In cases where this separation is not a good approximation, local population dynamics on the patch may also explicitly be modelled.

Besides local population dynamics, *environmental stochasticity* and *disturbances* may also play an important role for metapopulation dynamics. Environmental stochasticity refers to stochasticity of population parameters such as extinction risks or the hostility of the matrix. Reasons for this may be fluctuations in food availability or changing weather conditions. Similar to that, disturbances are usually defined as larger and more sporadic events that may pose strong or even catastrophic impacts on the population. It has been shown that spatial and temporal characteristics of environmental stochasticity and disturbances have a crucial impact on population dynamics (Hanski, 1999a; Johst et al., 2002).

### Recolonization through dispersal

Unpopulated patches may be recolonized through dispersal from occupied patches. The probability that a dispersal event leads to a successful recolonization of an unoccupied patch depends on a number of factors. The most basic assumption would be that, once an individual leaves its patch, it is subject to a constant mortality risk which would lead to an exponential decay of the probability of arrival as a function of the distance between patches. The probability $p_{ij}$ of arriving at patch $j$ after dispersing from patch $i$ is then described by an exponential dispersal kernel

$$p_{ij} = e^{-d_{ij}/l} \tag{2.1}$$

with $d_{ij}$ being the distance between patches, and $l$ being the typical dispersal distance of the species under consideration. More complicated dispersal kernels arise when dispersal includes individuals search behavior, perception range or viewing angle.

The probability of successful colonization of patch $j$ per time step is then given by some function of the sum of arriving individuals

$$c_j = f\left(\sum_i p_{ij} \cdot r_i\right) . \tag{2.2}$$

where $r_i$ is the amount of dispersing individuals from patch $i$.

### Landscape dynamics

Finally, there are processes which do not directly act at the population level, but rather on the patches themselves. Patches may for some reason lose their habitat quality and therefore disappear, and new habitats may appear elsewhere, for example through succession or through human disturbances. Landscape dynamics, which refer to these changes of the network, are usually discussed separately from disturbances, which refer to events that cause the extinction of a local population while leaving the patch intact. The effect of landscape dynamics and disturbances on populations, however, is often very similar. As an example, if the patch number is not too small and patches are randomly distributed, the repeated random removal of a patch and the creation of a new patch elsewhere is largely identical to an increase of local extinction rates (Hanski, 1999a).

## 2.2.3 Measures of population viability

Like most explicitly stochastic population models, the metapopulation models that were used in this thesis are Markov-models. In Markov-models, any state of the model contains the full information about future states, i.e. for calculating the next time step of the model, only knowledge about the present state is necessary. Because Markov-models are stochastic, they usually do not converge to one particular steady state, but they may have a stochastic equivalent to a steady state that is called the stationary distribution. The stationary distribution is the probability density function of states that is mapped to itself by the Markov-model.

One peculiarity of metapopulation models is that there is a state (zero population size) that may eventually be reached from any state, but that can never be left after it has been reached. In Markov-models, such a state is called an absorbing state. Therefore, the real stationary distribution of a metapopulation model with non-vanishing extinction probabilities is the state where the population size is zero, because this state will eventually be reached by any model run. More interesting than the extinct state, however, is the so-called quasi-stationary state. This state is, broadly speaking, the stationary state of the surviving Markov-chains that have not yet encountered the absorbing state (Dickman and Vidigal, 2002), i.e. something like the steady state of the model as long as the population has not gone extinct. Again, the existence of such a quasi-stationary state is due to a separation of time scales: Metapopulation dynamics, that is the dynamics of local extinction and recolonization are much faster than the process of total extinction, and thus model runs may converge to a quasi-stationary distribution, which then slowly fades into the real stationary distribution of zero population size. The transition of the quasi-stationary distribution to the absorbing state has the following properties:

- The transition rate from the quasi-stationary distribution to the absorbing state is constant.
- Therefore, the cumulative survival probability of the quasi-stationary state declines exponentially with time, and either the decay parameter of the exponential function (mean time to extinction), or the cumulative number of extinction events after a certain time is a sufficient statistics for describing the decay.

An example of this exponential decay can be seen in Fig. 2.4, top row.

### The (intrinsic) mean time to extinction

Analyzing the stability of metapopulation models, the typical approach is to perform a large number of model runs with fixed or stochastic starting conditions, and to observe the distribution of extinction events in time as a function of model parameters such as patch size or landscape connectivity. A problem of this analysis, however, is that the quasi-stationary distribution of the model is normally not known. Therefore, the sample of Markov-chains with which the model is initialized needs a certain time to reach the quasi-stationary distribution. During this time, the model is in the so-called transient state. For measuring extinction probabilities, it is important to know when the system has reached the quasi-stationary state, because the survival probabilities during the transient state will typically be different from the probabilities in the quasi-stationary state (Fig. 2.4, bottom row) , which may bias estimates of the steady state survival. As Grimm and Wissel (2004) note, in this cases the logarithmic cumulative distribution of extinction events is a more robust measure to analyze population survival because it allows to detect the length of the transient state: If the model is in equilibrium, a logarithmic histogram of extinction events should show a linear decline. Deviations from this linear decline after initialization mean that the model has not yet reached the quasi-stationary distribution. In some cases, such non-equilibrium effects may be the object of the study (see Hanski and Ovaskainen, 2002; Ovaskainen and Hanski, 2003), but in a steady state analysis transient effects should be removed. After doing so, the remaining data may be used to extract unbiased values for the mean time to extinction.

### Other output measures

Persistence and changes in persistence may be difficult to measure if the populations are in a very good condition. The reason is that, at very high survival probabilities, the necessary sampling effort for reaching appropriate statistical support to distinguish between two alternative model settings increases strongly. In such cases, measures like population size, patch occupancy or variance, which are assumed to be correlated with population persistence, may be used instead.

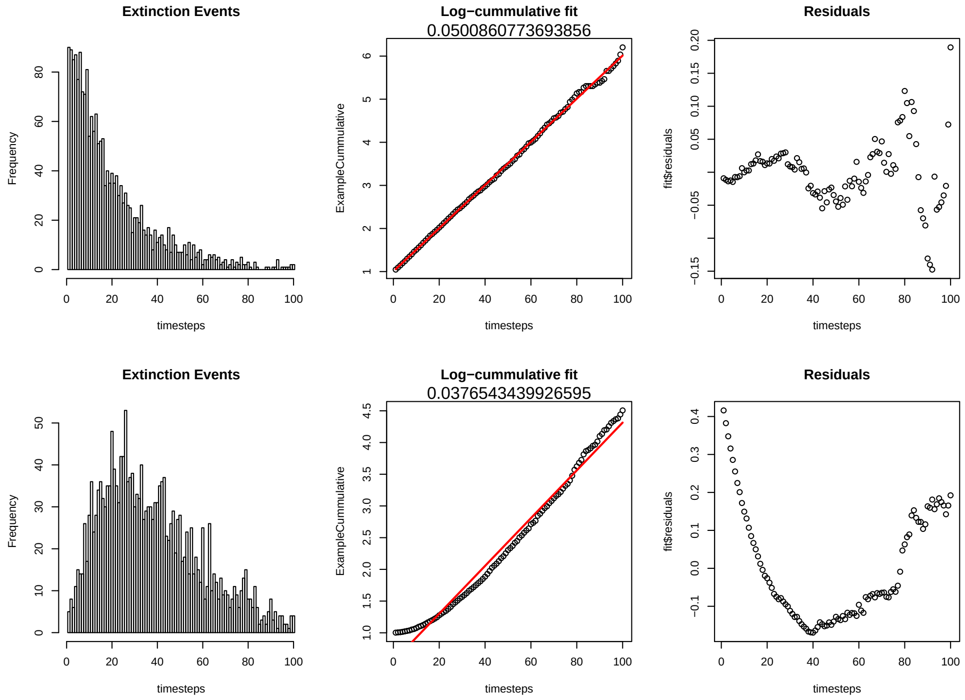


**Figure 2.4:** Intrinsic mean time to extinction: The plot shows the difference between a simulation that is initialized in the steady state (top row), and a simulation that exhibits a transient state of lower extinction probability (bottom row). The effect of this transient state appears in the histogram of extinction events (left), the logarithmic cumulative distribution (middle) and the residuals of the linear fit to the logarithmic cumulative distribution (right). If these measures show clear signs of transient effects, the fit of the logarithmic cumulative distribution is a more robust estimator of survival than the survival probability after a certain time (Grimm and Wissel, 2004).

### 2.2.4 General results from metapopulation research

Although the diversity of possible metapopulation models disqualifies general rules, there is a number of general results that will hold true for most simple single species metapopulation models.

#### Extinction thresholds and trade-offs between network properties

The general rule of thumb for macroscopic network properties such as the number of habitat patches, the network area or the network connectivity is: More is better. An important result from metapopulation research is that this "more is better" does not follow a linear relationship. If macroscopic network properties, such as patch number or connectivity, fall below certain thresholds, metapopulation survival decreases rapidly, while well above the threshold, the metapopulation is practically stable (Drechsler, 1994; Hanski et al., 1996; Hanski and Ovaskainen, 2000; Ovaskainen and Hanski, 2003).

The values of network properties for which critical thresholds appear are often interacting with each other. For instance, a decline in the number of patches may to a certain extent be compensated by larger patch areas. Thus, there are trade-offs between those macroscopic network properties, which can be specified as a function from a $n$-dimensional space of network properties to the survival probabilities of a species (Frank and Wissel, 2002; Drechsler, 2009).

### The role of disturbances and landscape dynamics

The most simple assumption for disturbances and landscape dynamics is that they happen uncorrelated in time. Yet, many environmental processes, such as weather, floods or fire may lead to correlated disturbances in space and possibly also in time. Fire, for example, is less likely to occur after a recent fire event because of the lack of fuel and thus shows a negative correlation in time. The opposite may be true for weather, which is often found to be positively correlated on short time scales. Generally, correlated disturbances are found to be more harmful than uncorrelated disturbances (see e.g. Johst and Drechsler, 2003; Kallimanis et al., 2005). However, it should be stressed that this applies for a single species metapopulation only. If multiple species are competing, a particular species may well have an advantage over another species at a certain disturbance regime and could therefore experience negative effects if the disturbance was removed. In many ecosystems, we find that an intermediate amount of disturbances facilitates the highest number of coexisting species. This is usually referred to as the intermediate disturbance hypothesis (Grime, 1973; Connell, 1978; Hobbs and Huenneke, 1992). In any case, disturbances and disturbance correlations may have a major effect on the estimated survival risks of stochastic population models. Consequently, we found in paper 2 that landscape dynamics created by the application of a conservation policy were an influential factor for the success of this policy.

## 2.3 Markets for conservation

The reason why landowners do not conserve their land is that they can gain higher profit from alternative land use. Changing their land use to conservation implies a cost for them. Such costs, that result from foregone benefits of alternative use, are called *opportunity costs*. The systematic inclusion of costs has only in recent years become increasingly used in planning methods. It is now widely accepted that the effectiveness of conservation schemes can be significantly improved when local land prices are taken into account (Ando et al., 1998; Polasky et al., 2005), and a lot of recent work has focussed on the inclusion of local costs to conservation (Faith and Walker, 1996; Ando et al., 1998; Wätzold and Schwerdtner, 2005) into conservation plans. However, getting reliable information about the spatial distribution of opportunity costs itself is very costly and difficult. The reason is that foregone benefits may not only differ due to physical reasons such as land quality, but also due to socio-economic factors such as individual preferences, capabilities and transaction costs. The latter factors are particularly difficult to extract because landowners have incentives to overstate their costs if they expect compensation payments for themselves. Therefore, reliable cost information is often unavailable for spatial conservation planning, which limits the efficiency of this approach.

An alternative to top-down approaches such as spatial planning is presented by conservation markets. Market-based instruments are characterized by one major idea: Instead of planning the allocation of conservation measures, the conservation market passes on the positive and negative external effects of land use actions to the land users. Doing so, landowners should automatically adjust their land use such that it is optimal from a global perspective, because they have the information about the distribution of local costs, which is unavailable to conservation planners (Jack et al., 2008).

Market-based instruments are currently being used or tested in many countries around the world. Some examples are conservation and wetland mitigation banking in the US (Salzman and Ruhl, 2000; Wilcove and Lee, 2004; Fox and Nino-Murcia, 2005) or market schemes in Australia (Coggan and Whitten, 2005; Latacz-Lohmann and Schilizzi, 2005). Broadly, market-based instruments fall into two classes: Price-based and quantity-based mechanisms (Weitzman, 1974). Price-based mechanisms such as payments (Wunder, 2007; Drechsler et al., 2007; Engel et al., 2008) offer a fixed price for conservation actions. Fixing the price of conservation implies that, unless the regulating authority is omniscient, the quantity of conservation produced at the chosen price is uncertain. Quantity-based mechanisms such as auctions (Latacz-Lohmann and Van der Hamsvoort, 1998) or biodiversity offset schemes (Panayotou, 1994; Chomitz, 2004) fix the quantity of conservation produced by the scheme, at the costs of being uncertain about the prices that are necessary to reach the quantity.

Market implementations may differ in their degree of complexity and transaction costs for conservation authorities and market participants, but also in the level of cost-effectiveness that can be reached. When deciding on which instrument is used for creating a market for conservation services, authorities usually face a number of objectives: More detailed ecological metrics, an increase of monitoring and enforcement, and the use competitive prices mechanisms such as auctions promise a higher effectiveness. On the other hand, transaction costs and acceptance problems (Frey, 1992) of regulating authorities and landowners may reduce or outweigh these advantages and suggest more simple schemes. The following subsection summarizes the advantages and disadvantages of different market-based conservation instruments. Fig. 2.5 shows an overview of the discussed market mechanisms.

### 2.3.1 Price-based incentives: payments and taxes

One of the easiest and therefore most widely applied tools for conservation on private lands are fixed payments or fees for environmental services (Wunder, 2007; Engel et al., 2008). Broadly speaking, this includes payment schemes, but also subsidies, taxes and agri-environmental schemes (AES), where a fixed amount of money is offered conditional on certain metrics or other indicators that are directly or indirectly linked to conservation objectives.

Price-based incentive schemes are relatively easy to organize for authorities and transparent for landowners who know exactly how much money they will get for a certain conservation measure. There are, however, also two economic disadvantages of price-based schemes:

- **Producer surplus**: Price-based schemes usually apply the same price to all landowners - this means that payments have to be adjusted to the highest costs that still need to be included in the scheme. All participants who have lower costs profit from what is called the producer surplus. Although this money is not lost for the economy, but simply transferred from conservation authorities to landowner, this has distributional consequences because the money will be used for different purposes than biodiversity conservation.
- **Determining the right payment level**: It is often difficult to determine the price that is necessary to reach a certain target beforehand. The reason is the information asymmetry between conservation authorities and market participants - while landowners know their costs, conservation authorities can only estimate them, or draw conclusions from participation rates in previous market schemes.

Uncertainty about the right price level implies that conservation authorities are uncertain both about the costs and the amount of participation created by policy. One could limit the amount of financed measures to reduce this uncertainty. This, however, only allows an upper limit on costs, while particularly too low participation rates are deleterious for the conservation success. Also, such limits bear additional problems of equity between landowners and increased producer surplus.

The disadvantages of flat rate payments can be mitigated if some information about the costs of land owners is available. In this case, payments can be adjusted according to the different costs of landowners, for example according to the size of the measure, the soil type, etc. (Wätzold and Drechsler, 2005; Wünscher et al., 2008). Yet, such information is seldom easily available, and social considerations such as equity and fairness may discourage individually adjusted payments.

### 2.3.2 Quantity-based incentives: auctions

One way to avoid the problem of finding the right price are auctions (Wu and Babcock, 1996; Latacz-Lohmann and Van der Hamsvoort, 1998; Latacz-Lohmann and Schilizzi, 2005). A common auction form for conservation actions is a reverse auction - here, a conservation authority would announce the willingness to finance a certain amount of measures, and individuals can submit their bids by stating an amount that they would be willing to accept as a payment for such a measure. Competition among landowners promises bid prices that are close to the individual opportunity costs for conservation.

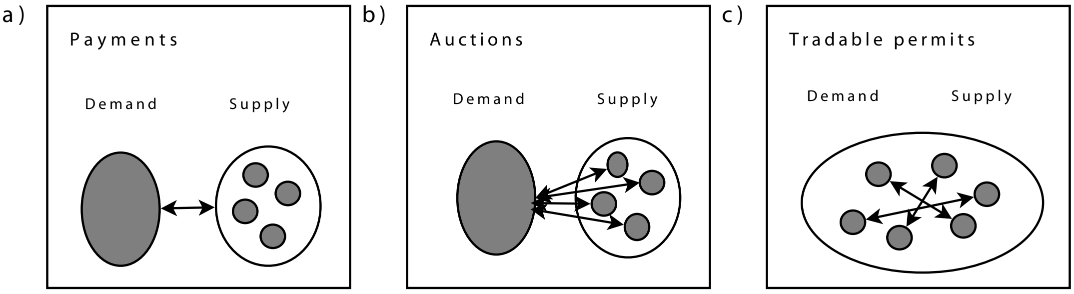


**Figure 2.5:** Conservation markets: a) In a payment scheme, there is one fixed price that is offered e.g. by a conservation authority to market participants. b) In an auction, there may be many, variable prices and individual transactions between a conservation authority and the supplying market participants. c) In a tradable permit scheme, each market participant can be on the demand side as well as on the supply side, depending on his costs relative to the costs of other market participants.

Thus, as long as suppliers face sufficient competition, the conservation authority does not need to estimate opportunity costs, but the auction mechanism adjusts prices for conservation such that they meet the target supply.

Auctions offer considerable advantages for conservation authorities. In contrast to payments, they are a quantity-based instrument, meaning that conservation authorities can decide on the extent of financed measures beforehand. Also, they promise lower transfers to landowners, as the problem of information asymmetry and producer surplus is likely to be mitigated. The main disadvantage of auctions is that they are difficult to organize and involve higher transaction costs for regulating authorities and landowners. Therefore, they rather qualify for larger measures that involve higher costs, for which the advantages of more competitive prices outweigh the increased transaction costs.

### 2.3.3 Quantity-based incentives: tradable permits

A second quantity-based instrument that aims at creating competition between conservation suppliers and thereby promises to allocate conservation to the most cost-effective locations are tradable permits. Unlike in auctions, demand within a tradable permit scheme does not come from a conservation authority. Demand is induced by creating an obligation for each market participant to provide a certain amount of conservation actions. If market participants overfulfill their obligation, they are credited this in the form of a permit. Other market participants can buy such permits to compensate for underfulfilling their obligation. Examples of tradable permits include the carbon emissions trading schemes settled under the Kyoto Protocol or the tradable permit system for restricting emissions of ozone-depleting chemicals in the US after 1988 (Tietenberg, 2006).

In recent years, tradable permit schemes with names such as biobanking or biodiversity credit trading have also been suggested or applied to restrict land use and ensure the maintenance of natural habitats and biodiversity (Chomitz, 2004; Wissel and Wätzold, 2008; Drechsler and Wätzold, 2009). In such a scheme, landowners who wish to decrease the conservational value of their land need a permit. These permits can be acquired from landowners that have voluntarily increased the conservational value of their land. Thus, whether market participants decide to buy or to produce permits depends on their costs for conservation relative to other market participants.

## 2.4 Individual decisions

Human land use patterns are neither homogenous nor random. Fig. 2.6 shows a land use map created by a simulation model of future land use in the Netherlands (paper 5). It is clearly visible that some land use types tend to cluster. Also, geographical and physical conditions affect the chosen land use types. When trying to understand how humans react to certain policy incentives, it is important to understand how land use decisions evolve.

For the moment let us assume that all land is owned by someone. Ownership of land usually implies the right to control its use, the right to any benefits originating from the property, or the right to transfer or sell the property. Most societies, however, have put limits to the property rights associated with the ownership of land. It is for example very common that building activities require permission from local governments.

### 2.4.1 Maximizing individual utility

Within their property rights, landowners choose the land use option that delivers the highest benefit to them. Benefits could be monetary if landowners engage in some form of commercial land use, such as agriculture or mining, but they could also be non-monetary such as preferences for keeping an area in a natural state. We call the perceived total benefit or total satisfaction that results from all positive or negative benefits $b_i$ associated with a certain action or decision its *utility* $U$ and write

$$U = g(b_i) \tag{2.3}$$

Here, $g(b_i)$ is some function of the benefits $b_i$. Although landowners decide individually on the use of their land, utilities and thus land use decisions are highly influenced by the land use in their surrounding. A motorway for example decreases the utility of using land in the direct vicinity for housing, fast access to a motorway, however, may increase the utility of land for housing on a particular site.

### 2.4.2 Land use changes and discounting

Changing land use is usually costly. Costs may e.g originate from the construction of infrastructure of a necessary change of physical properties of the land. Nevertheless, alternative land use may still pose potential benefits which outweigh those costs and

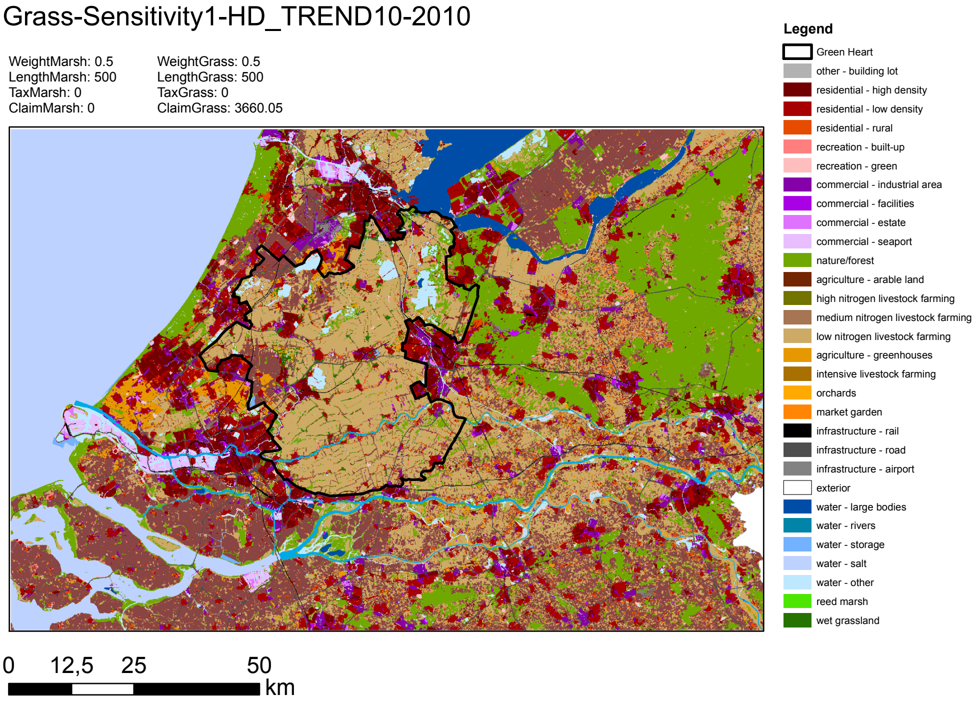


**Figure 2.6:** Land use: The map shows a prediction of land use under a particular environmental policy in the Netherlands (paper 5).

make a change desirable. Costs and benefits which do not arise at the same time can therefore not simply be subtracted. In economics, comparing costs or benefits which do not appear at the same time uses the method of *discounting* (Heal, 2007). Discounting assumes that individuals may have time preferences for receiving goods or services. The typical assumption is that individuals prefer receiving goods and services earlier, and that they do so at a constant rate, i.e. that a good has only $100\% - \delta$ of its value if it is received one year later. The factor $\delta$ is called the discount-factor. In continuous time, changing costs and benefits can then be discounted to a single value by

$$U = \int_0^\infty u(t) \cdot f(t)\, dt \tag{2.4}$$

where $u(t)$ are utilities at time $t$, and $f(t)$ is the applied *discounting function*. For the case of a constant time preference as discussed above, the discount function is simply an exponential function where the discount rate $\delta$ is the decay parameter:

$$f(t) = e^{-\delta \cdot t} \,. \tag{2.5}$$

Both the shape and the parameters of the discounting function are highly debated in economics, in particular because the exact form of the discounting function impacts

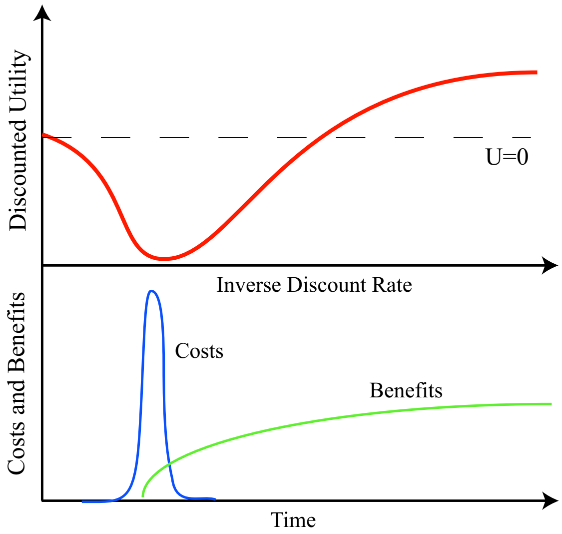


**Figure 2.7:** The dependence of utility on discount rates: The lower curve shows a temporal distribution of costs and benefits. The upper curve shows the discounted utility as a function of the inverse of the applied discount rate. The inverse discount rate $\delta^{-1}$ can be interpreted as a indicator of the time horizon of the decision.

heavily on the evaluation of long term damages such as could be expected from climate change. For one thing, there is considerable spread in what is perceived as an appropriate discount rate (Henderson and Sutherland, 1996; Stern et al., 2006; Nordhaus, 2007). Also, although exponential discounting remains the standard assumption, there is some evidence that long term discounting deviates from an exponential shape in favor of hyperbolic shapes (Frederick et al., 2002). Fig. 2.7 shows an illustration of the concept of discounting.

### 2.4.3 Externalities

A further important aspect of individual decisions for the allocation of land use are *externalities*, also called *spillovers*. An externality is a cost or a benefit that is created by the decision of one party and posed on a party that is not directly involved in the decision process. Externalities are a major concern in markets, because they may lead to inefficient allocation of resources. Externalities can be classified in bilateral, multilateral or public good externalities (Fig. 2.8) depending on how the involved parties interact. Also, one may classify spatial or temporal externalities. The above mentioned construction of a motorway, which changes land use benefits in its surrounding and thus creates a spatial externality on neighboring landowners, is an example of a spatial externality. Another example is climate change, which creates a temporal externality because current actions generate costs that will appear in the future.

There is some debate in economics about when externalities need correction. Coase

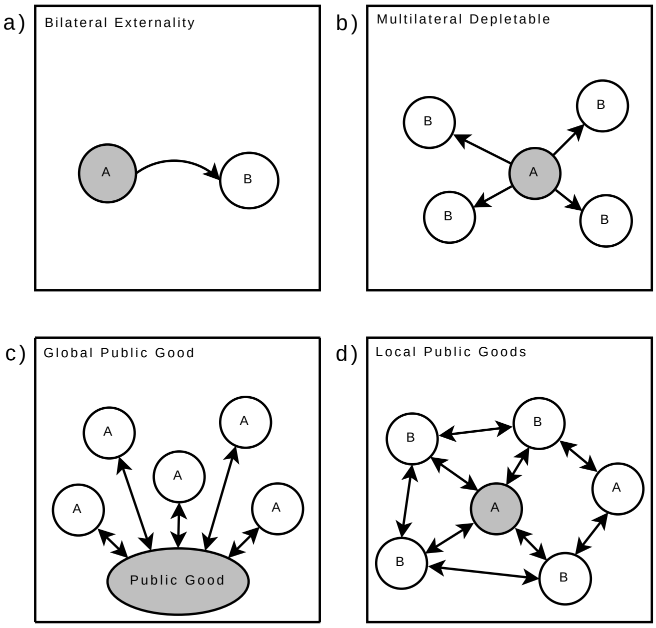


**Figure 2.8:** Types of externalities: a) A bilateral externality is a cost or benefit that is posed from one party to another. b) A multilateral externality is posed from one party to many parties. c) A public good/bad is a benefit/cost that is experienced by all parties. d) Finally, local public goods may be spatially confined to smaller regions.

(1960) argued that bargaining between the involved parties will efficiently resolve externality problems if property rights are well defined, individuals act rationally and transaction costs (i.e. the costs of bargaining) are low. Yet, this is often not the case for environmental goods and services, particularly those which are common and public goods. Therefore, an important concern of market-design is the reduction of externalities by legislation, taxes or subsidies. We show in paper 4 that this is also an important concern for conservation markets with spatial incentives, because these markets account for externalities between sites that are created by the benefits caused by the presence of habitat in the vicinity of other habitats.

## 2.5 Combining metapopulations, markets and individuals

### 2.5.1 Quantifying ecological benefits

The first step to a systematic conservation program is to decide on the ecological goals of conservation (Margules and Pressey, 2000). Say, for example, we would like to spend a certain amount of money on the protection of primates. Probably everyone would agree that lowering the extinction risk of the endangered Mountain Gorilla in Africa is a beneficial conservation outcome. But, given a limited budget, should it all be spent now, trying to reach conservation benefits fast, or should we reserve money for a later time to ensure persistence in the long run? Also, are we really worried about persistence, or are we rather valuing the presence and visibility of a species in a certain region? For example, tourists of a national park may not only value the survival, but also the visibility of the gorilla. Moreover, although there is probably little debate that the protection of the Mountain Gorilla would be beneficial, so would be the protection of the Sumatran Orangutan. How should we split our money?

One of the most straightforward measures of conservation success is the survival probability of a species as a function of different conservation options. This method is known as *population viability analysis*. We have used population viability as indicator for conservation success throughout our research (papers 1, 2, 4).

### Trade-offs between species

Yet, even if we have agreed on survival as the sole indicator of conservation success, from the moment that we target more than one species, we face the problem of defining a *trade-off* between them (Nicholson and Possingham, 2006; Bottrill et al., 2008). This means that we first have to decide whether those targets are *commensurable*, i.e. if we would tolerate the decrease of one species for the increase of another or several other species, and secondly, if they are commensurable, we have to define the trade-off, i.e. the exchange rate between species survival probabilities.

One means to do so is defining combined objective functions. Picking up on the discussion about the protection of apes, one could for instance decide that the survival of either of them is equally important, but a decrease in survival probability of one of the species can be compensated by an increase of survival probability of the other. The combined objective is then given by

$$U = p_1 + p_2. \tag{2.6}$$

where the $p_1$ and $p_2$ are the survival probabilities of the respective ape species. Such an objective, however, implies that the compensation for a particular species is largely independent of its current state. If this is not desired, one may use other functions, which increase compensation for the rare species, such as the following equation:

$$U = \sqrt{p_1} + \sqrt{p_2}\,. \tag{2.7}$$

We have discussed these as well as associated problems in paper 1.

A way to visualize trade-offs are *indifference curves*. An indifference curve marks the combinations of the two targets that are valued equally. Fig. 2.9 shows indifference curves for the two objective functions eqs. 2.6 and 2.7.

### Societal time preferences

One question is *what* we set as a target, the other is *when*. For example, are we trying to preserve a species for the next generation, for the next three, or forever? How are

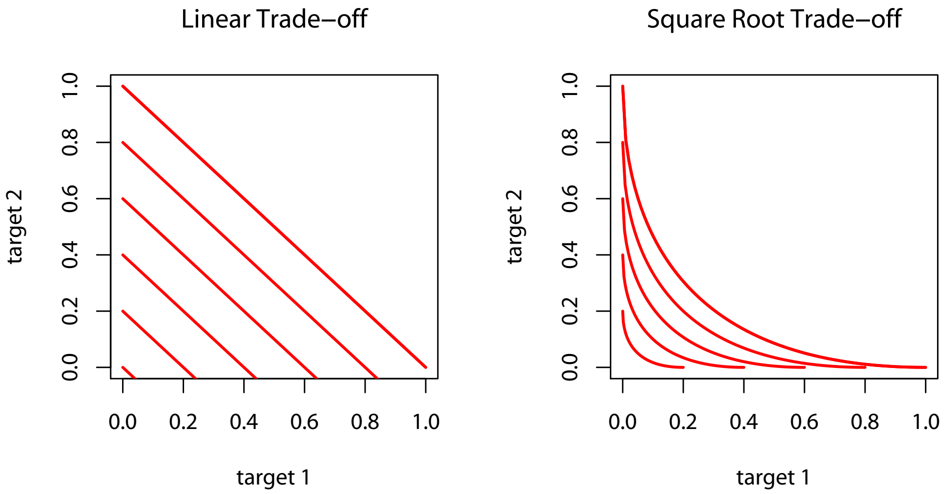


**Figure 2.9:** Indifference curves for two environmental objectives given in eqs. 2.6 and 2.7: The x-axis displays the supply level of target 1, the y-axis the supply level of target 2. The indifference curves mark the combinations of the two targets that are valued equally. Given a linear trade-off, the loss of a unit of target 1 can always be compensated by one unit of target 2. Thus, the relative compensation, also called the marginal rate of substitution, is constant. In the square root trade-off, the compensation depends on the current level of each target. Here, the marginal rate of substitution is not constant: The rarer target 1, the more compensation of target 2 is needed to allow for a decrease in target 1.

impacts of climate change weighted if they are likely to occur only in one generation, while there are other threats that unfold their impacting right now? There has been a lot of debate on the right choice of time preferences in the context of climate change and conservation (Rabl, 1996; Weitzman, 1998; Heal, 2007). In paper 1, we contributed to this discussion by showing that time preferences can have a major impact on the evaluation of conservation decisions when there are trade-offs such as those in eqs. 2.6 and 2.7.

### 2.5.2 Measures of effectiveness

In the preceding section, we have discussed how to quantify conservation benefits. To decide which conservation actions are preferable, however, we need to consider not only their benefits, but also their costs. If benefits and costs are known in monetary units, one would simply select all conservation actions for which the benefits are higher than the costs. It is, however, difficult and controversial to translate population viability into monetary units, and we excluded the option of cost-benefit analysis in our approach. If benefits of conservation are known, but not in monetary terms, it is not possible to

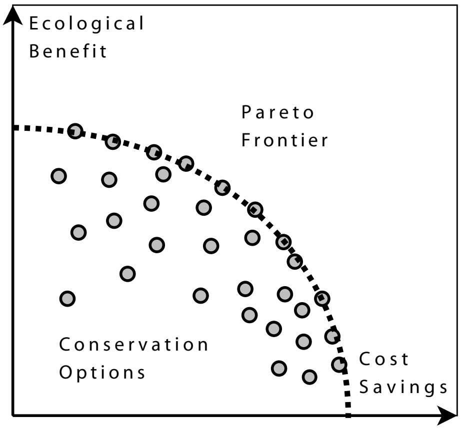


**Figure 2.10:** Pareto frontier of economic and ecological benefits: Each conservation option is drawn in a plane according to its monetary benefits, that is cost savings (x-axis) and its (non-monetary) conservation benefits (y-axis). For all values that have equal costs (x-axis), the one with the highest benefits is most cost-effective. Similarly, for all values that have equal ecological benefits (y-axis), the one with the highest cost-savings is most cost-effective. The concept behind this is Pareto-optimality: A point is Pareto-optimal, if there is no other point that is better in both cost savings and conservation benefits. This enables us to draw a frontier of Pareto-optimal points. This frontier is often referred to as the possibility frontier, the efficiency frontier, or simply the Pareto frontier. Each point of the Pareto-frontier is cost-effective and Pareto-optimal. A comparison between Pareto-optimal points, however, is beyond the scope of a cost-effectiveness analysis and would require to merge costs and environmental benefits into one currency, for example into monetary units.

give an absolute ranking of conservation options. However, within all options that have the same costs, the option that has the highest conservation benefit is clearly preferable. Similarly, among all the options with the same conservation benefits, the option with the lowest cost is clearly preferable. Fixing either the costs or the benefits in this manner is called a *cost-effectiveness analysis*. Cost-effective are the options that are Pareto-superior in the space of costs and effects. Fig. 2.10 shows an illustration of this.

Throughout our research, we have chosen cost-effectiveness as measure of the efficiency of conservation policies (Paper 2, 4). Using population viability as indicator for conservation success, it is straightforward to apply cost-effectiveness when being concerned with only one species. For the cases of several species, we combined survival probabilities of the examined species through a trade-off function, as discussed in paper 1.

### 2.5.3 Designing and optimizing market-based policies

Having discussed how to include costs and benefits of conservation to one measure of effectiveness, the last part of this section discusses how to use such a measure to compare and optimize the design of market-based conservation policies. We explain several methods such as optimization, agent-based models, and inverse policy optimizations.

### Global optimization

Given that we have a measure of effectiveness, we can use optimization methods to find the best possible habitat configuration(s) under the current costs and benefits of conservation. Global optimization methods for conservation, often referred to as reserve site selection or prioritization, have attracted a lot of research (see Cabeza and Moilanen, 2001, for an overview). Yet, despite a lot of technical advances in optimization methods, the systematic application of optimization has not found widespread application in practice. One reason is that, although computational barriers have been pushed forward in recent years, large scale optimization still puts limitations to the model complexity that can be optimized, and often requires simplifying assumptions, which limit the practical reliability of the optimization results. Another reason is that appropriate input data for optimizations is difficult to generate, in particular on the side of the opportunity costs - when trying to enforce a particular landscape structure, landowners may demand much higher compensations than calculated and thus change the assumptions that were the base for the global optimization. Nevertheless, if good data is available, optimization measures are a valuable tool to inform planners about beneficial conservation options. We used optimization in paper 4 to compare the land use allocations generated by an agent-based model with the globally optimal allocation.

### Agent-based models

While global optimizations are useful to inform global planners about the most efficient allocation(s) of conservation measures, their usefulness for estimating the outcomes of policy instruments that give incentives to a large number of individuals is limited. There is a number of reasons why individual decisions do not have to be globally optimal. Among them are individual variations in preferences, bounded rationality or, as mentioned in 2.4.3, externalities. Thus, when trying to optimize policies for conservation on private lands, approaches that model decisions on an individual level are more appropriate.

Agent-based models (ABMs), similar to individual-based models (IBMs) in ecology, describe the behavior of a larger economic system bottom up by describing the behavior and interactions of individuals. In these models, effects of externalities, bounded rationality, individual differences in costs or incomplete information can be quantified explicitly. Thus, it is possible to explicitly check for robustness of conservation policies under those effects. We used agent-based models in paper 2 and paper 4.

### Game theory

A second approach, which explicitly focuses on situations where individuals interact, is game theory. Game theory analyzes individual behavior in situations where the success of individuals depends on the choices of other individuals. While ABMs allow quantifying

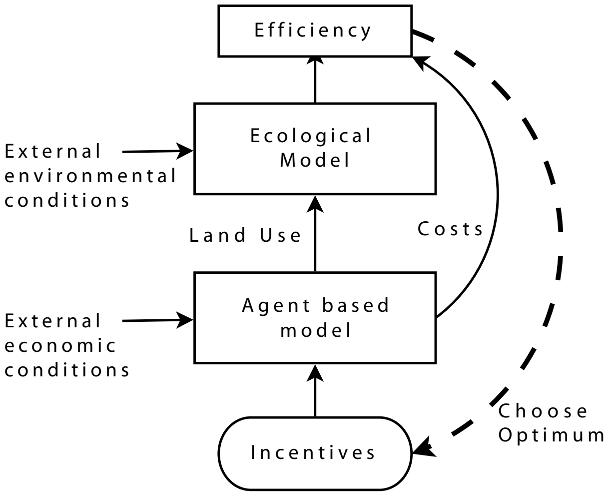


**Figure 2.11:** Inverse policy optimization: For the set of all possible policy incentives, the economic model calculates costs and land use choices. Based on those land use choices, the ecological simulations predict the survival probabilities of the targeted species within this landscape. Combining costs and survival probabilities, policy measures can be filtered for the most effective measures.

the outcomes of actions of many individuals with particular strategies, game theory aims at explaining why individuals are using particular strategies in a certain situation. A particular interest of game-theoretical studies are situations where the optimal strategy from the individual viewpoint (individual rationality) does lead to suboptimal decisions from the global viewpoint (group rationality). The tragedy of the commons, which was mentioned in the introduction, is one example of such a social dilemma. Game theory can aid a better understanding of the mechanisms that encourage or discourage selfish behavior and thus help to design policy instruments that are more robust towards market failures due to free riding or exploitation of public goods. We used game theoretical arguments in paper 2 and paper 3.

### Inverse policy optimization

Given that we have both economic models, which predict landowners' land use choices under market-based conservation incentives, and ecological models, which predict species reaction to these land use choices, we can combine these models to optimize the incentives of a conservation market. The way to do this is sketched in Fig. 2.11: For a set or all possible policy incentives, the economic model calculates costs and land use choices. Based on those land use choices, the ecological simulations predict the survival probabilities of the targeted species within this landscape. Combining costs and survival probabilities, policy measures can be filtered for the most effective measure, or displayed as a possibility frontier as shown in Fig. 2.10. This approach, which we call *inverse policy optimization*, was used in paper 2.

# Chapter 3

# Research Papers

## List of papers in this chapter

paper I

Florian Hartig, Martin Drechsler

# The time horizon and its role in multiple species conservation planning

**Biological Conservation, 2008, 141, 2625-2631**
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**Summary:** We show that conservation recommendations based on additive multiple-species objective functions are sensitive to the choice of the time horizon of the objective function.

BIOLOGICAL CONSERVATION 141 (2008) 2625–2631

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# The time horizon and its role in multiple species conservation planning

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ABSTRACT

Survival probability within a certain time horizon $T$ is a common measure of population viability. The choice of $T$ implicitly involves a time preference, similar to economic discounting: conservation success is evaluated at the time horizon $T$, while all effects that occur later than $T$ are not considered. Despite the obvious relevance of the time horizon, ecological studies seldom analyze its impact on the evaluation of conservation options. In this paper, we show that, while the choice of $T$ does not change the ranking of conservation options for single species under stationary conditions, it may substantially change conservation decisions for multiple species. We conclude that it is of crucial importance to investigate the sensitivity of model results to the choice of the time horizon or other measures of time preference when prioritizing biodiversity conservation efforts.

## 1. Introduction

A central problem for conservation planning is the decision on conservation goals (Margules and Pressey, 2000). These goals are used to define quantitative objective functions, which are needed for a systematic comparison of conservation options (see e.g. Wilson et al., 2006). Depending on societal preferences, a number of ecosystem properties and services may be valued, and objective functions may vary accordingly (Balvanera et al., 2001; Williams and Araujo, 2002; Roberts et al., 2003). For conservation planning, objectives built on measures such as percentage of preserved area or expected coverage are traditionally used because they are relatively easy to apply; however, it has been repeatedly shown that these measures may fail to act as a reliable surrogate for the persistence of species (Cabeza and Moilanen, 2003; Svancara et al., 2005; Wiersma and Nudds, 2006). Species survival probabilities, in contrast, provide a measure which relates directly to the actual goal of persistence and thus acts as a better predictor for conservation success (Williams and Araujo, 2000; Guisan and Thuiller, 2005).

Translating the goal of persistence into a quantitative objective based on survival probabilities needs some further clarification when dealing with multiple species. A number of different objective functions are used in the literature. Some maximize the expected number of surviving species, others use the probability of all species surviving, or the probability of the most threatened species surviving (see e.g. Bevers et al., 1995; Nicholson and Possingham, 2006). Although all aiming at improving species survival, these objectives may vary substantially in their rating of conservation options and subsequently in their choice of conservation priorities (Nicholson and Possingham, 2006).

Despite their differences, all these functions express survival in terms of the probability of surviving until some time $T$. $T$, frequently called the time horizon or the time

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frame, is a preferred time at which conservation success is evaluated. A short time horizon acts similarly to a large discounting factor in economics and vice versa. While the choice of such time preferences is subject to serious debate in the field of environmental economics (Rabl, 1996; Weitzman, 1998; Heal, 2007), it seems that conservation planning has widely neglected this topic so far. Some of the rare exceptions include Eisworth and Haney (2001) and Cabeza and Moilanen (2003). One explanation may be that the time horizon usually has no impact on static single species conservation, and it is believed that the same holds true for multi-species conservation. Another reason may be that the controversy about discounting ecological values has been considered a social science issue much more than an ecological question. Nevertheless, our results show that excluding this discussion from the scope of conservation planning may result in misleading and possibly unintended conservation recommendations.

In this paper, we analyze three typical objective functions which are used in the literature with respect to their sensitivity to the choice of the time horizon. We find that, for additive functions, this choice may have a crucial impact on the resulting conservation decisions. We conclude that the choice of a time horizon is an inevitable part of decision making. Its influence must be borne in mind and should be explicitly communicated when determining conservation targets.

## 2. Methods and assumptions

### 2.1. The time horizon and annual survival

Under stationary environmental conditions (no trends in population parameters such as carrying capacity, so that the population is in a quasi-stationary state), the probability of surviving until time T is given by

$$p(T) = e^{-\frac{T}{T_m}} \tag{1}$$

where $T_m$ is the mean time to extinction (Grimm and Wissel, 2004), measured in years. The annual survival probability is $x = \exp(-1/T_m)$. With Eq. (1), we can then express the survival of a species until time T by

$$p(T) = x^T \tag{2}$$

where x denotes the annual survival probability as given before. Using this as the basis of our evaluation, we should first note a trivial, but crucial fact: the survival probability p decreases nonlinearly (exponentially) with the time horizon T. For a stationary single species case under stationary external conditions, however, this nonlinearity does not change ratings based on the survival probability p; given that a conservation option has a higher $p(T_0)$ than another option for a time horizon $T_0$, it will also have a higher $p(T)$ for any other time horizon T.

### 2.2. Multi-species objective functions

For the case of multiple species, knowledge of single species survival probabilities is not enough to compare conservation options. As an example, imagine the case of two species, and two conservation alternatives, one which yields survival probabilities of $p_1 = 70\%$ and $p_2 = 90\%$, and another which results in $p_1 = 80\%$ and $p_2 = 80\%$. Which option is to be preferred? The expectation value of the number of species surviving, $p_1 + p_2$, is the same for both cases. Yet, the second conservation alternative shows a more even distribution of survival probabilities between species.

The literature has approached the problem of multi-species survival mainly with two classes of objective functions: additive and multiplicative ones (see Nicholson and Possingham, 2006). In its most simple form, an additive objective function for n species is given by the sum of the single species survival probabilities $p_i$:

$$\sum_{i=1}^{n} p_i \tag{3}$$

Mathematically, the sum represents the expected value of the number of species surviving. Examples of studies using additive functions are Faith and Walker (1996), Polasky et al. (2001), Nicholson et al. (2006). A simple multiplicative function is given by the product of all survival probabilities:

$$\prod_{i=1}^{n} p_i \tag{4}$$

This product represents the probability that all species survive (see e.g. Bevers et al., 1995). Multiplicative objective functions tend to favor an even distribution of survival probabilities, whereas additive objectives generally do not (Nicholson and Possingham, 2006). In the context of biodiversity, such an evenness objective is often considered advantageous. However, it is also possible to include evenness objectives in additive objective functions (see e.g. Arponen et al., 2005; Moilanen, 2007). As an example of such a function, we chose the p-norm:

$$\left(\sum_{i=1}^{n} p_i^{\alpha}\right)^{1/\alpha} \tag{5}$$

This function weights each single species survival probability with $p_i^{\alpha}$, and then adds these values up. For $0 < \alpha < 1$, the weighting favors an even distribution of survival probabilities, and for $\alpha = 1$ it is identical to the additive function. In a broad sense, Eq. (5) resembles the Shannon index, which is often used to express biodiversity as a function of species abundance. A summary of the three objective functions is given in Table 1.

### 2.3. The relation between costs and species survival

Ideally, the question of conservation priorities would not have to be asked, and we would simply provide each species with sufficient and adequate resources and habitat for their survival. Unfortunately, conservation is only one of many competing human ambitions. In the majority of

**Table 1 – Overview of the analyzed objective functions**

| Function | Objective |
|---|---|
| $\sum_{i=1}^{n} p_i$ | Expected number of surviving species after T |
| $\prod_{i=1}^{n} p_i$ | Probability of all species surviving after T |
| $(\sum_{i=1}^{n} p_i^{\alpha})^{1/\alpha}$ | Sum of weighted survival probabilities |

situations, systematic conservation planning is subject to a limited budget B, and it has to be decided how this budget is spent most effectively (Naidoo et al., 2006; Wilson et al., 2006).

This decision is further complicated because the relationship between costs spent on conservation and resulting change in population survival is often not linear. On the one hand, it is very frequently found and assumed that the costs for additional conservation increase with increasing conservation efforts (see e.g. Eisworth and Haney, 2001; Drechsler and Burgman, 2004; Naidoo et al., 2006). For example, land may get increasingly scarce and therefore more expensive when the areas used for conservation are increased (Drechsler and Watzold, 2001; Armsworth et al., 2006; Polasky, 2006). On the other hand, conservation efforts often need to cross certain thresholds, such as the minimal viable population size, to become effective (With and Crist, 1995; Hanski et al., 1996; Fahrig, 2001).

A function which may conveniently exhibit all theses characteristics and which is therefore often used to model threshold situations is the sigmoid function (Fig. 1). We use this function to illustrate our findings, however, all general results of this paper will not depend on the particular functional form, but only on general curvature properties of the cost–survival function. For now, let us assume that an amount $b_i$ of our conservation budget B will increase the annual survival rate $x_i$ of the ith single species according to

$$x_i = \frac{1}{1 + e^{-a_i \cdot (b_i + c_i)}} \tag{6}$$

where $a_i$ controls the steepness of the threshold and $c_i$ represents the initial state of the species, i.e. the value which is achieved without any budget expenditures. Eq. (6) grows convexly (more than linearly, Fig. 1A) below the threshold (when $c_i + b_i < 0$) and concavely (less than linearly, Fig. 1B) above the threshold (when $c_i + b_i > 0$). Note that for sufficiently small steepness a ($a \ll 1/B$), the cost–survival function can be considered approximately linear (Fig. 1C), a fact that will be used in the following analysis. Furthermore, we assume that species do not interact and do not share any common resources or habitats. Thus, $x_i$ does not depend on $b_j$ with $i \neq j$.

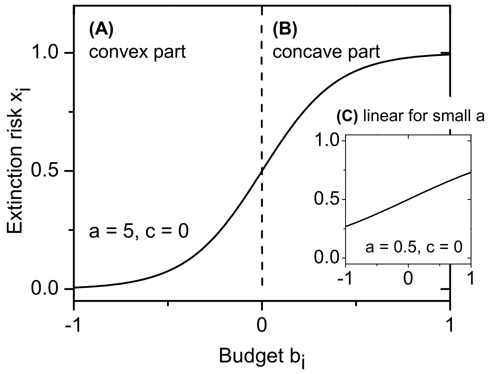

**Fig. 1 – Relationship between budget expenditure and survival of a single species for Eq. (6) with $a = 5$, $c = 0$. (A) Below the threshold, Eq. (6) is convex. (B) Beyond the threshold, Eq. (6) is concave. (C) For $a \ll B^{-1}$, Eq. (6) is approximately linear.**

### 2.4. *The optimal conservation decision*

To compare the conservation decisions which would be made based on the discussed objective functions (Eqs. (3)–(5)) and different time horizons T, we assume the following:

A landscape planner has to split a budget B between two species. He spends $b_1$ on species 1 and $b_2 = B - b_1$ on species 2. We call the case where most of the budget is used for one species an uneven distribution, and we call the case where the budget is spent evenly among the two species an even distribution. The annual survival probability of each species changes with $b_i$ according to Eq. (6). The survival probability after the time horizon T is given by Eq. (2). Inserting this into the three objective functions (additive, multiplicative, p-norm), we calculate the value of the objective functions (the score) for time horizons between 1 and 100 years, $b_1$ ranging from 0% to 100% of the budget B, and different functional relationships between annual survival probability $x_i$ and budget expenditure $b_i$.

## 3. Results

Analyzing the model, it becomes evident that the effect of the time horizon depends on the relation between budget expenditures and species survival. To illustrate this, we discuss the results for four different scenarios: first, we present the results for species survival of both species depending linearly, concave (less than linearly) and convex (more than linearly) on budget expenditures. Finally, we discuss a case where the two species are in a different initial state and thus react differently to budget expenditures.

### 3.1. *Linear cost–survival functions*

For species survival depending linearly on budget expenditure (as, e.g., in Fig. 1C), we obtain the following scores as a function of T and the budget distribution: for the additive objective, we find the highest scores for uneven distributions, spending all of the budget on one of the two species. In contrast, the multiplicative objective favors an even distribution throughout all choices of the time horizon T. Finally, the p-norm favors an even distribution for short time horizons until a critical time $T_c$. For any T larger than $T_c$, uneven distributions are favored. The results are displayed in Fig. 2.

### 3.2. *Concave cost–survival functions*

For a concave relationship between budget expenditure and annual survival probability we observe, both for the additive and the p-norm objectives, a change of conservation priorities around a critical time $T_c$. For time horizons smaller than $T_c$, an even budget distribution is favored, while at larger T uneven distributions rate best. Again, the multiplicative objective favors an even distribution for all choices of T. The results are displayed in Fig. 3.

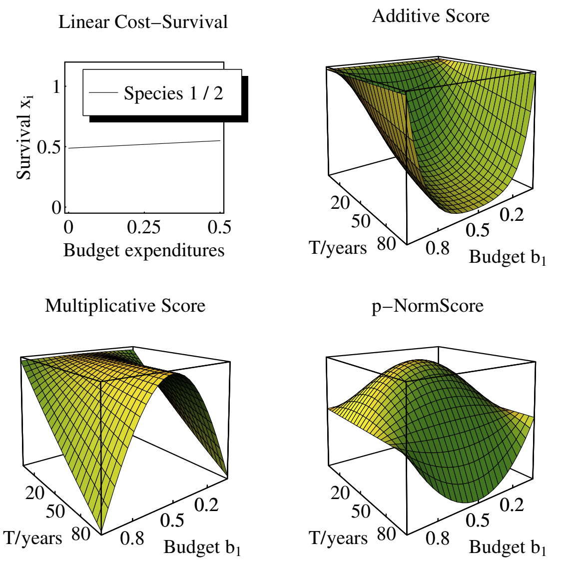

**Fig. 2 – Linear cost–survival function: the three 3-d plots show the score for the additive, the multiplicative, and the *p*-norm objective function. On the *x*-axis (right) the proportion of the budget assigned to species 1, on the y-axis (left) the time horizon *T* in years, and on the *z*-axis (upwards) the score of the respective conservation option. Parameters: $a = 0.4$, $B = 0.5$, $c = -0.1$, $\alpha = 0.013$. For each *T*, the *z* values are scaled to a reference value (the score that would be obtained by choosing $b_1 = 0$ for additive and *p*-norm functions, and $b_1 = 0.5$ for the multiplicative function) to allow the graph to be more easily read. Otherwise, cases of high *T* would hardly be visible because survival probabilities here are naturally lower than for cases of small *T*.**

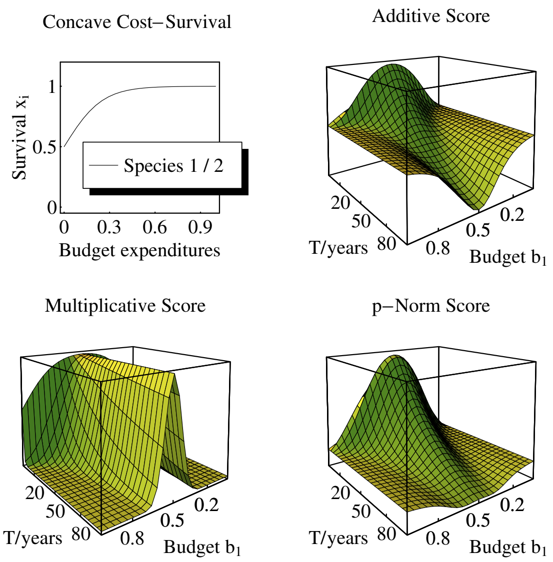

**Fig. 3 – Concave cost–survival function: the three 3-d plots show the score for the additive, the multiplicative, and the *p*-norm objective function. On the *x*-axis (right) the proportion of the budget assigned to species 1, on the y-axis (left) the time horizon *T* in years, and on the *z*-axis (upwards) the score of the respective conservation option. Parameters: $a = 8$, $B = 1$, $c = 0$, $\alpha = 0.5$. For each *T*, the *z* values are scaled as in Fig. 2 to allow the graph to be more easily read.**

### 3.3. *Convex cost–survival functions*

Convex cost–survival functions naturally favor uneven budget distributions, owing to the more than linear growth of survival with the budget expenditure. For moderate convexity, however, the results still resemble the linear case (Fig. 2) very closely. Only for a very strong convexity may the balancing influence of the multiplicative and the *p*-norm function eventually be overruled, and all three objectives favor an uneven distribution for any time horizon $T > 1$.

### 3.4. *Non-even baseline values*

Finally, we show a case with different initial states for the two species: species 1 has a poor initial state of conservation below the threshold (convex cost–survival, see Fig. 1A), and species 2 is above the threshold and in a much better initial state (concave cost–survival, see Fig. 1B). The resulting scores are shown in Fig. 4: both for the additive and the *p*-value functions, the score favors a concentration on the threatened species 1 for short time horizons and a concentration on the more stable species 2 for long time horizons. Under a multiplicative objective, conservation budgets are always concentrated on the threatened species.

### 3.5. *Generalization of the results*

Are these results general, or only valid for a small or unreasonable parameter range? As we show in Appendix A, conservation decisions with additive functions like Eqs. (3) and (5) are in fact sensitive to the time horizon under quite general conditions, which is that either: (a) the functional relation between budget expenditures and survival is sufficiently concave; or (b) the multi-species objective function puts a sufficiently strong weight on even survival probabilities and the relationship between costs and survival is concave, linear, or sufficiently weakly convex.

Equally important, however, is whether such a sensitivity of conservation decisions will appear in real world situations. To examine the sensitivity of the model to changes in the parameters, we solved numerically for the time where conservation decisions shift between even and uneven budget distributions. The results (Appendix B) show that the parameter range which yields a switch within the range of typical choices for *T* is fairly large.

In contrast to additive objective functions, we could not find any impact of *T* whatsoever for the case of the multiplicative function. This is no coincidence, but can easily be understood. Since the power operation commutes with the multiplication, a conservation alternative that maximizes

$\prod_i x_i$ also maximizes $\prod_i p_i$ for any $T$. Therefore, a simple multiplicative function with a static budget is not influenced by the choice of the time horizon. A formal proof of this is given in Appendix C.

## 4. Discussion

Evaluating multi-species survival probabilities requires the choice of an objective function which transforms survival probabilities into a single value. Different forms of objective functions have been used in the literature, some of which maximize the expected number of surviving species (additive functions), whereas others also emphasize an even distribution of survival probabilities among species (multiplicative functions or weighted additive functions).

Our results show that the time horizon at which species survival probabilities are calculated has a crucial impact on conservation decisions with additive functions when at least one of the following two assumptions is fulfilled: (a) the functional relation between budget expenditures and survival is sufficiently concave; or (b) the multi-species objective function puts a sufficiently strong weight on even survival probabilities and the relationship between costs and survival is concave, linear, or sufficiently weakly convex. For our simple case of two species, conservation decisions based on such functions change drastically when the time horizon crosses some critical value $T_c$.

The underlying reason behind this is that survival probability drops exponentially with the time horizon. While a concave cost–survival relationship or a concave objective function favor an even budget distribution for short time horizons, the exponential decay makes small differences very large in the long run and therefore eventually shifts the highest score to uneven distributions when the time horizon $T$ is increased. This time-dependence of the indicator “survival probability” constitutes a major difference to other indicators, such as expected coverage, which are used for conservation planning.

Our sensitivity analysis revealed that a crucial influence of the time horizon appears for a large range of realistic parameter combinations and functions. Therefore, a potentially drastic influence of $T$ on conservation decisions for practical cases cannot be ruled out. Only multiplicative functions showed no response to the choice of $T$ at all. This is no coincidence, but a fundamental property of multiplicative functions, as we showed. However, we do not believe that this is necessarily an argument in favor of multiplicative functions. A multiplicative function is certainly useful when the survival of all species is the main goal, but its absolute insistence on evenness can make it a dangerous choice when the budget is not large enough to conserve all species. For such cases, it may be that a distribution of the budget that maximizes a multiplicative objective minimizes the expected number of species surviving (e.g. Fig. 2).

In conclusion, we believe that the influence of time preferences on conservation decisions has not been appreciated enough in the past. This is even more so given that a lot of recent research is attracted by dynamical problems which are by their nature strongly affected by the choice of the time horizon (Meir et al., 2004; Drechsler, 2005; McBride et al., 2007; Pressey et al., 2007). As we increasingly realize that the future challenges for conservation such as climate and global change are dynamic, time preferences will play an increasing role in conservation decisions. Thus, the time horizon must be acknowledged as a fundamental part of the objective function. It should be selected with care, and its influence should be analyzed and communicated when presenting conservation recommendations.

But what is the right time horizon? Ultimately, the choice of a time horizon is a normative decision. It cannot be decided on scientifically, but must be developed in interaction with stakeholders and society. To establish such an interaction, the influence of the time horizon has to be determined and openly communicated.

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## Appendix A. Proof of the time dependence of additive functions

Assume we have two species with equal cost–survival functions. We get an even distribution as a unique solution if the summands of the objective function which are given by

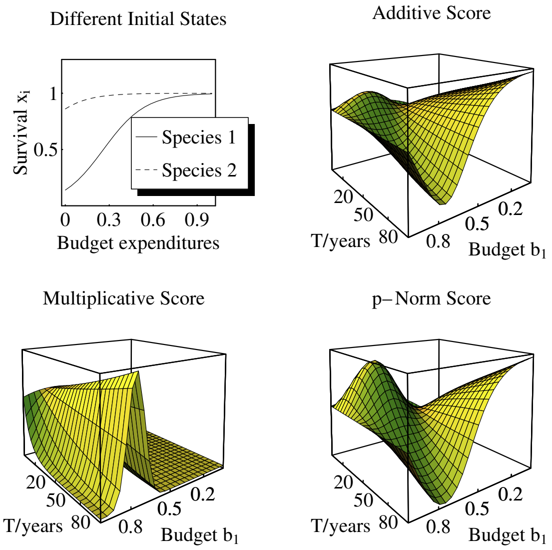

**Fig. 4 – Different initial states: the three 3-d plots show the score for the additive, the multiplicative, and the *p*-norm objective function. On the *x*-axis (right) the proportion of the budget assigned to species 1, on the *y*-axis (left) the time horizon *T* in years, and on the *z*-axis (upwards) the score of the respective conservation option. Parameters: $a = 7$, $B = 1$, $c_1 = -0.26$, $c_2 = +0.26$, $\alpha = 0.5$. The values for the two additive objective functions are scaled as in Fig. 2, the values for the multiplicative objective are scaled at each *T* to the value obtained by $b_1 = 0.82$.**

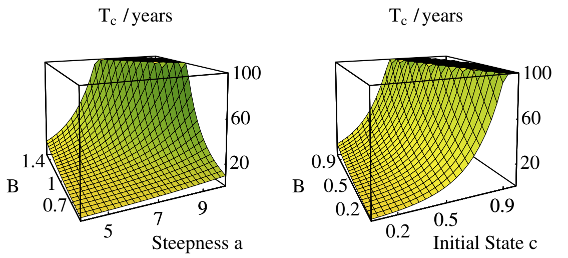

**Fig. 5 – $T_c$, the time horizon where the highest score changes from an even to an uneven budget distribution as functions of *a*, *B* and *c*. Other parameters: $c = 0$ (left panel), $a = 5$ (right panel). The cost–survival function corresponding to the right panel ($a = 5$) is shown in Fig. 1.**

$$(x(b))^{\alpha\cdot T} \tag{A.1}$$

are concave functions of *b* on the whole domain accessible with the budget *B*. Accordingly, we get an uneven distribution as a unique solution if Eq. (A.1) is convex on the whole domain. Assuming that the cost–survival function is a smooth function of *b*, all derivatives are bounded and there will be a $T_{\min}$ such that Eq. (A.1) is concave for all $T < T_{\min}$ and a $T_{\max}$ such that Eq. (A.1) is convex for all $T > T_{\max}$. Thus, the optimal budget distribution must switch or exhibit multiple solutions between $T_{\min}$ and $T_{\max}$. The same argument also applies for species with different cost–survival functions with the addition that optimal points may slightly shift position as can be seen in Fig. 4.

Hence, there will always be a range of *T* at which Eq. (A.1) changes from a concave to a convex function and we may observe a dramatic shift of optimal conservation decisions. For practical considerations, however, this will only be of relevance if the critical time $T_c$ where the highest score switches from even to uneven distributions, is within the range of typical choices for the time horizon *T* (30–100 years). From Eq. (A.1), we see directly that this can only be the case if there exists a *T* within the considered range such that (a) $x(b)$ is sufficiently concave to compensate the convex influence of $\alpha \cdot T$ in the exponent of Eq. (A.1) or (b) $x(b)$ is concave, linear, or sufficiently weakly convex and $\alpha < 1$ is sufficiently small to make Eq. (A.1) linear within the considered range.

## Appendix B. Sensitivity analysis

To get an estimate of the sensitivity of the time $T_c$ where the budget distribution changes towards a change of parameters, let us assume we have an additive objective function, equal initial states $c_i$ and equal concave cost–survival functions. Then $T_c$ will be approximately at the time *T* where the score of a totally uneven distribution of the budget equals the score of an even distribution:

$$x(B)^{T_c} + x(0)^{T_c} = 2 \cdot x(B/2)^{T_c} \tag{B.1}$$

Here, $(B, B/2, 0)$ refers to the proportion of the budget *B* to be inserted in the cost–survival function Eq. (6). We solved Eq. (B.1) numerically with the sigmoid function Eq. (6). Fig. 5 shows that the range of parameters which yield times $T_c$ between 1 and 100 years is fairly large.

## Appendix C. Proof of the time-independence of a multiplicative score

The multiplicative score Eq. (4) can be rewritten as

$$\prod_i p_i = \prod_i (x_i)^T = \left(\prod_i x_i\right)^T \tag{C.1}$$

As the power operations commute with the multiplication, we can factor out the power operation. The latter is strictly monotonous, hence an option which maximizes $\prod_i x_i$ also maximizes $\prod_i p_i$ for any *T*.

## REFERENCES

Armsworth, P.R., Daily, G.C., Kareiva, P., Sanchirico, J.N., 2006. From the cover: land market feedbacks can undermine biodiversity conservation. Proceedings of the National Academy of Sciences of the United States of America 103 (14), 5403–5408. doi:10.1073/pnas.0505278103.

Arponen, A., Heikkinen, R.K., Thomas, C.D., Moilanen, A., et al, 2005. The value of biodiversity in reserve selection: representation, species weighting, and benefit functions. Conservation Biology 19 (6), 2009–2014. doi:10.1111/j.1523-1739.2005.00218.x.

Balvanera, P., Daily, G.C., Ehrlich, P.R., Ricketts, T.H., Bailey, S.-A., Kark, S., Kremen, C., Pereira, H., 2001. Conserving biodiversity and ecosystem services. Science 291 (5511), 2047. doi:10.1126/science.291.5511.2047.

Bevers, M., Hof, J., Kent, B., Raphael, M.G., 1995. Sustainable forest management for optimizing multispecies wildlife habitat: a coastal douglas-fir example. Natural Resource Modeling 9, 1–23.

Cabeza, M., Moilanen, A., 2003. Site-selection algorithms and habitat loss. Conservation Biology 17 (5), 1402–1413. doi:10.1046/j.1523-1739.2003.01421.x.

Drechsler, M., 2005. Probabilistic approaches to scheduling reserve selection. Biological Conservation 122 (2), 253–262. doi:10.1016/j.biocon.2004.07.015.

Drechsler, M., Burgman, M.A., 2004. Combining population viability analysis with decision analysis. Biodiversity and Conservation 13 (1), 115–139. doi:10.1023/B:BIOC.0000004315.09433.f6.

Drechsler, M., Watzold, F., 2001. The importance of economic costs in the development of guidelines for spatial conservation management. Biological Conservation 97 (1), 51–59. doi:10.1016/S0006-3207(00)00099-9.

Eiswerth, M.E., Haney, J.C., 2001. Maximizing conserved biodiversity: why ecosystem indicators and thresholds matter. Ecological Economics 38 (2), 259–274. doi:10.1016/S0921-8009(01)00166-5.

Fahrig, L., 2001. How much habitat is enough? Biological Conservation 100 (1), 65–74. doi:10.1016/S0006-3207(00)00208-1.

Faith, D.P., Walker, P.A., 1996. Integrating conservation and development: effective trade-offs between biodiversity and cost in the selection of protected areas. Biodiversity and Conservation 5 (4), 431–446. doi:10.1007/BF00056389.

Grimm, V., Wissel, C., 2004. The intrinsic mean time to extinction: a unifying approach to analysing persistence and viability of populations. Oikos 105 (3), 501–511. doi:10.1111/j.0030-1299.2004.12606.x.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8 (9), 993–1009. doi:10.1111/j.1461-0248.2005.00792.x.

Hanski, I., Moilanen, A., Gyllenberg, M., 1996. Minimum viable metapopulation size. American Naturalist 147 (4), 527–541.

Heal, G., 2007. Discounting: a review of the basic economics. University Of Chicago Law Review 74 (1), 59–77.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405 (6783), 243–253. doi:10.1038/35012251.

McBride, M.F., Wilson, K.A., Bode, M., Possingham, H.P., 2007. Incorporating the effects of socioeconomic uncertainty into priority setting for conservation investment. Conservation Biology 21 (6), 1463–1474. doi:10.1111/j.1523-1739.2007.00832.x.

Meir, E., Andelman, S., Possingham, H.P., 2004. Does conservation planning matter in a dynamic and uncertain world? Ecology Letters 7 (8), 615–622. doi:10.1111/j.1461-0248.2004.00624.x.

Moilanen, A., 2007. Landscape zonation, benefit functions and target-based planning: unifying reserve selection strategies. Biological Conservation 134 (4), 571–579. doi:10.1016/j.biocon.2006.09.008.

Naidoo, R., Balmford, A., Ferraro, P.J., Polasky, S., Ricketts, T.H., Rouget, M., 2006. Integrating economic costs into conservation planning. Trends in Ecology and Evolution 21 (12), 681–687. doi:10.1016/j.tree.2006.10.003.

Nicholson, E., Possingham, H.P., 2006. Objectives for multiple-species conservation planning. Conservation Biology 20 (3), 871–881. doi:10.1111/j.1523-1739.2006.00369.x.

Nicholson, E., Westphal, M.I., Frank, K., Rochester, W.A., Pressey, R.L., Lindenmayer, D.B., Possingham, H.P., 2006. A new method for conservation planning for the persistence of multiple species. Ecology Letters 9 (9), 1049–1060. doi:10.1111/j.1461-0248.2006.00956.x.

Polasky, S., 2006. You can't always get what you want: conservation planning with feedback effects. Proceedings Of The National Academy Of Sciences Of The United States Of America-Physical Sciences 103 (14), 5245–5246. doi:10.1073/pnas.0601348103.

Polasky, S., Camm, J.D., Garber-Yonts, B., 2001. Selecting biological reserves cost-effectively: an application to terrestrial vertebrate conservation in oregon. Land Economics 77 (1), 68–78.

Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M., Wilson, K.A., 2007. Conservation planning in a changing world. Trends in Ecology and Evolution 22 (11), 583–592. doi:10.1016/j.tree.2007.10.001.

Rabl, A., 1996. Discounting of long-term costs: what would future generations prefer us to do? Ecological Economics 17 (3), 137–145. doi:10.1016/S0921-8009(96)80002-4.

Roberts, C.M., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J., Halpern, B.S., Lafferty, K.D., Leslie, H., Lubchenco, J., McArdle, D., Ruckelshaus, M., Warner, R.R., 2003. Application of ecological criteria in selecting marine reserves and developing reserve networks. Ecological Applications 13 (1), S215–S228. doi:10.1890/1051-0761(2003)013[0215:AOECIS]2.0.CO;2.

Svancara, L.K., Brannon, R., Scott, J.M., Groves, C.R., Noss, R.F., Pressey, R.L., 2005. Policy-driven versus evidence-based conservation: a review of political targets and biological needs. Bioscience 55 (11), 989–995.

Weitzman, M.L., 1998. Why the far-distant future should be discounted at its lowest possible rate. Journal of Environmental Economics and Management 36 (3), 201–208. doi:10.1006/jeem.1998.1052.

Wiersma, Y.F., Nudds, T.D., 2006. Conservation targets for viable species assemblages in Canada: are percentage targets appropriate? Biodiversity and Conservation 15 (14), 4555–4567.

Williams, P.H., Araujo, M.B., 2000. Using probability of persistence to identify important areas for biodiversity conservation. Proceedings of the Royal Society of London Series B-Biological Sciences 267 (1456), 1959–1966. doi:10.1098/rspb.2000.1236.

Williams, P.H., Araujo, M.B., 2002. Apples, oranges, and probabilities: integrating multiple factors into biodiversity conservation with consistency. Environmental Modeling and Assessment 7 (2), 139–151. doi:10.1023/A:1015657917928.

Wilson, K.A., McBride, M.F., Bode, M., Possingham, H.P., 2006. Prioritizing global conservation efforts. Nature 440 (7082), 337–340. doi:10.1038/nature04366.

With, K.A., Crist, T.O., 1995. Critical thresholds in species responses to landscape structure. Ecology 76 (8), 2446–2459.

paper II

Florian Hartig, Martin Drechsler

# Smart spatial incentives for market-based conservation

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**Summary:** We find that conservation incentives which account for connectivity are more cost-effective than purely area-based incentives and we show how connectivity incentives can be optimized for single and multiple species.

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# Smart spatial incentives for market-based conservation

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ABSTRACT

Market-based instruments such as payments, auctions or tradable permits have been proposed as flexible and cost-effective instruments for biodiversity conservation on private lands. Trading the service of conservation requires one to define a metric that determines the extent to which a conserved site adds to the regional conservation objective. Yet, while markets for conservation are widely discussed and increasingly applied, little research has been conducted on explicitly accounting for spatial ecological processes in the trading. In this paper, we use a coupled ecological–economic simulation model to examine how spatial connectivity may be considered in the financial incentives created by a market-based conservation scheme. Land use decisions, driven by changing conservation costs and the conservation market, are simulated by an agent-based model of land users. On top of that, a metapopulation model evaluates the conservational success of the market. We find that optimal spatial incentives for agents correlate with species characteristics such as the dispersal distance, but they also depend on the spatio-temporal distribution of conservation costs. We conclude that a combined analysis of ecological and socio-economic conditions should be applied when designing market instruments to protect biodiversity.

## 1. Introduction

Market-based instruments such as payments (Wunder, 2007; Drechsler et al., 2007), auctions (Latacz-Lohmann and Van der Hamsvoort, 1998) or biodiversity offset trading (Panayotou, 1994; Chomitz, 2004) have been suggested as a means to complement existing reserves by inducing biodiversity protection on private lands. Market-based instruments are currently being used or tested in many countries around the world. Some examples are conservation and wetland mitigation banking in the US (Salzman and Ruhl, 2000; Wilcove and Lee, 2004; Fox and Nino-Murcia, 2005) or market schemes in Australia (Coggan and Whitten, 2005; Latacz-Lohmann and Schilizzi, 2005). One of the reasons for the increasing popularity of these instruments is the realization that markets may achieve a more targeted and therefore more cost-efficient correction of a conservation problem, in particular because landowners have more information about their local costs and can choose the allocation of conservation measures accordingly (Jack et al., 2008). Another reason is that market-based instruments are well suited for targeting multiple ecosystem services, e.g. conservation and carbon sequestration (Nelson et al., 2008), a point which has been highlighted in a recent statement of the European Union (EU-Commission, 2007).

At the same time, however, there has been considerable concern over whether current implementations of conservation markets target the right entities. At present, market-based policies for conservation tend to use simple and indirect incentives, such as payments for certain farming practices (Ferraro and Kiss, 2002). But are those incentives efficient in protecting threatened species, or are we paying "money for nothing" (Ferraro and Pattanayak, 2006)? Examin-

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ing the structure of the given incentives for landowners is the key to answering these questions. What defines a unit of conservation? What are we paying landowners for?

The overall goal of global conservation efforts is to ensure the persistence of biodiversity in our landscapes (Margules and Pressey, 2000). Therefore, it would be ideal to assess the market value of a conservation measure directly by assessing its effect on species survival (Williams and Araujo, 2000; Bruggeman and Jones, 2008). Unfortunately, applying this method to real-world situations is often not feasible because direct monitoring or detailed population models are too expensive or not available (Jack et al., 2008). Moreover, the efficiency of markets crucially depends on the information available to landowners. If landowners do not understand the evaluation criteria for their land, they may choose suboptimal land configurations, or they may decide not to participate in the market at all. Therefore, practically all existing market schemes use a metric, given by a number of indices, that relates measurable quantities of a site (e.g. size) to the site's market value.

Most of these existing schemes base their evaluation solely on the quality and size of the local site without considering its surroundings. This raises some concern because in many cases, the ecological value of a typical private property (e.g. an arable field or a forest lot) does in fact depend on neighboring properties. Populations or ecosystems may exhibit thresholds for the effectiveness of conservation measures, which implies that a local measure may be ineffective when it is not accompanied by other measures (Hanski et al., 1996; Scheffer et al., 2001). Furthermore, for many endangered species, not only the absolute loss of habitat area, but also habitat fragmentation is a major cause of population decline (compare e.g. Saunders et al., 1991; Fahrig, 2002). Therefore, metrics that only evaluate sites locally may set the wrong incentives because they do not correspond to the real conservational value of a site.

Spatial metrics that consider the surrounding of a site are available and are widely used for systematic reserve site selection (e.g. Moilanen, 2005; van Teeffelen et al., 2006). Yet, simply transferring spatial metrics from conservation planning into connectivity-dependent incentives for landowners (in the following we will call such incentives short "spatial incentives") would be short sighted. Conservation planning metrics have been developed for assessing and optimizing the ecological value of a habitat network from the viewpoint of a planner who considers the whole landscape. Landowners in conservation markets, on the other hand, react to the given incentives independently and with limited knowledge, striving for maximization of their individual utility rather than maximizing global welfare. The fact that the value of a site depends on neighboring sites implies that land use decisions may create costs or benefits for neighboring landowners. In economics, such costs or benefits are referred to as externalities. It is well known that markets may fail to deliver an optimal allocation of land use in the presence of such externalities (Mills, 1980). Another problem is that, unless we assume perfect information and unlimited intellectual capacities, we must take into account that landowners may fail to find the optimal adoption of their land use in the presence of complicated spatial evaluation rules (Hartig and Drechsler, 2008a). Thus, the need to consider human behavior in metrics for market-based instruments is characterized by a trade-off: Ecological accuracy calls for a metric that is complex enough to capture all details of the relevant ecological processes, but socio-economic reality may suggest compromises towards more practical and robust metrics.

In this paper, we combine a spatially explicit population model with an agent-based simulation model to assess the effect of connectivity-dependent incentives in a virtual conservation market. One key assumption is that landowners do not react optimally to the given incentives, but base their decisions only on the present land configuration and their estimated costs and benefits for the next period. Thus, we seek to optimize for ecological parameters such as dispersal as well as for economic parameters such as behavior of landowners. To simulate the reactions of landowners towards a given spatial metric, we use the conservation market model introduced in (Hartig and Drechsler, 2008a). A spatially explicit metapopulation model is placed on top of the emerging landscape structure to evaluate the conservation success for different species in terms of survival probability at a fixed time horizon.

## 2. Methods

### 2.1. Overview and purpose

The aim of this study is to design spatial incentives that result in cost-effective conservation when there are many landowners and the conservation outcome depends on the combination of decisions by landowners. Here, cost-effective means that we maximize the conservation effect at a given budget. The model used contains two submodels: An economic submodel that simulates the trading of conservation credits and an ecological submodel to assess the viability of several species in the dynamic landscape that emerges from the trading activity. The driver for trading and the subsequent change of the landscape configuration is economic change in the region, reflected by heterogeneously changing costs of maintaining a local site in a conserved state. We first describe the state variables of the model, followed by the economic and the ecological submodel and the coupling of the submodels. The coupled model is then used to find the cost-effective metric by comparing the forecasted species persistence across a range of different parameterizations of the metric. Fig. 1 shows a graphical representation of our model approach.

### 2.2. State variables and scales

The simulation is conducted on a rectangular $30 \times 30$ grid with periodic boundary conditions (i.e. the grid has the topology of a torus). The $n = 30^2$ grid cells represent both the economic (property) units and the ecological (habitat) units. Although the model may be applied to any spatial and temporal scale, we think of grid cells as being of the size of an average agricultural field in Europe (around 10 ha), and time steps being a year. Grid cells $x_i$ occur in two states: They can be conserved at a cost $c_i$ and thus provide habitat for the species, or

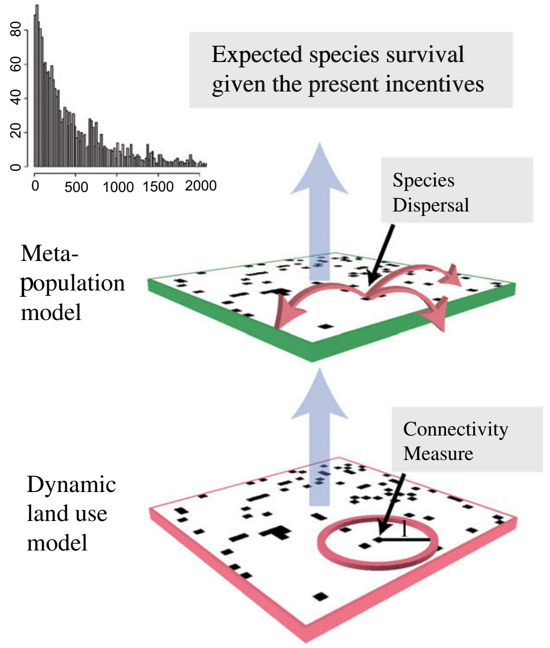


**Fig. 1 – Modelling approach: Drivers are spatially heterogeneous, dynamic costs for each site. On the basis of these costs and the spatial incentives, conservation measures are allocated by the economic submodel. The resulting dynamic landscape is used as an input for the ecological model, which estimates species survival probabilities on this landscape.**

**Table 1 – List of state variables (top), parameters of the economic model (middle), and parameters of the ecological model (bottom). Note that although we omit to denote the time dependence (t) explicitly throughout the main text, all state variables and expressions derived from state variables are time dependent.**

| Symbol | Connotation | Range |
|---|---|---|
| State variables: | | |
| $x_i$ | Position of the $i$th cell on the grid | |
| $\sigma_i(t)$ | Conservation state of the i-th cell | $\{0,1\}$ |
| $p_i(t)$ | Population state of the i-th cell | $\{0,1\}$ |
| $c_i(t)$ | Opportunity costs of $\sigma_i = 1$ at t | around 1 |
| Parameters economic model: | | |
| $\Delta$ | Cost heterogeneity | $[0..1]$ |
| $\omega$ | Cost correlation | $[0..\infty]$ |
| $m$ | Connectivity weight | $[0..1]$ |
| $l$ | Connectivity length | $[0..\infty]$ |
| $\lambda$ | Budget constraint | $[0..\infty]$ |
| Parameters ecological model: | | |
| $e$ | Local extinction risk | $[0..1]$ |
| $r$ | Emigration rate | $[0..\infty]$ |
| $r_d$ | Emigration rate after destruction | $[0..\infty]$ |
| $\alpha^{-1}$ | Dispersal distance | $[0..\infty]$ |

they are used for other economic purposes, resulting in no costs. The conservation state of a grid cell is labelled with $\sigma_i, \sigma_i = 1$ being a conserved cell and $\sigma_i = 0$ being an unconserved cell. Conserved grid cells may be either occupied (populated) $p_i = 1$ or unoccupied $p_i = 0$ by the species under consideration. Unconserved grid cells can never be occupied. A list of the state variables and parameters of the two submodels is given in Table 1.

### 2.3. *Economic model*

The economic model describes the decisions of landowners to establish, maintain, or quit a conservation measure on their land (grid cell) in each period. Landowners decisions are based on whether conservation or alternative land use generates a higher return. The returns on the two land use types are influenced by dynamic, spatially heterogeneous costs for conserving a grid cell and by the metric of the conservation market, which decides on the amount of conservation credits to be earned with a particular site, and by the current market price for conservation credits. The model is designed as a spatially explicit, agent-based partial equilibrium model (compare Drechsler and Wätzold, in press; Hartig and Drechsler, 2008a).

A conserved grid cell $x_i$ produces a certain amount of conservation credits $\xi_i$ depending on the number of conserved grid cells in its neighborhood. We use the following metric to determine $\xi_i$:

$$\xi_i = (1-m) + m \cdot \zeta_i(l). \qquad (1)$$

The first term $1-m$ is independent of the connectivity and may be seen as a base reward for the conserved area. The parameter $m$ is a weighting factor that determines the importance of connectivity compared to area. The second term $m \cdot \zeta(l)$ includes the connectivity of the site, measured by the proportion of conserved sites within a circle of radius $l$

$$\zeta_i(l) = \left(\sum_{d_{ij}<l} \sigma_j\right) \cdot \left(\sum\nolimits_{d_{ij}<l} 1\right)^{-1}. \qquad (2)$$

Here, $d_{ij}$ refers to the distance between the focal cell $x_i$ and another cell $x_j$. Fig. 2 shows a graphical illustration of this connectivity measure. The total amount of credits in the market is given by the sum of $\xi_i$ over all conserved grid cells

$$U = \sum\nolimits_{i=1}^{n} \sigma_i \xi_i. \qquad (3)$$

The conservation of a site results in costs that differ among grid cells. Conservation costs may vary over space

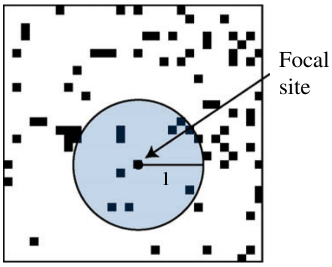


**Fig. 2 – Illustration of the connectivity measure: The connectivity $\zeta_i(l)$ is the fraction of conserved sites within a circle of radius $l$ of the focal site.**

and time (Ando et al., 1998; Polasky et al., 2008). We use three different algorithms to generate pattern of random dynamic costs $c_i(t)$. All algorithms create average costs of 1, but they differ in the spatial and temporal distribution of costs. Algorithm 1 generates spatially and temporally uncorrelated random costs by drawing from a uniform distribution of width $2\Delta$ at each time step. Algorithm 2 creates spatially uncorrelated, but temporally correlated costs by applying on each grid cell a random walk of maximum step length $\Delta$ together with a small rebounding effect that pushes costs towards 1 with strength $\omega$. Algorithm 3 creates spatio-temporally correlated costs, using a random walk of maximum step length $\Delta$ combined with a spatial correlation term that pushes costs with strength $\omega$ towards the average costs in the neighborhood. A mathematical description of the three algorithms is given in Appendix B.2, together with figures of the created cost distributions (Figs. 7 and 8).

To simulate trading, we introduced a market price $P$ for credits. The benefits to be earned by a site are given by $P \cdot \xi$ where $\xi$ is the amount of credits to be earned by a site (Eq. 1). Based on his costs and the potential benefits, each landowner decides whether to conserve his land or not. The model has two options for determining the equilibrium price of the market: Either the price is adjusted until a certain target level for the total amount of produced conservation credits $U$ (Eq. 3) is met, or the price is adjusted until a certain level of aggregated costs for the conservation is reached. By aggregated costs, we mean the sum of the costs of all conserved sites

$$C = \sum_{i=1}^{n} \sigma_i c_i. \tag{4}$$

Fixing the target reflects a situation where the quantity of conservation credits is fixed. This is, for example, the case in a tradable permit scheme. Fixing the costs, on the other hand, could correspond to a payment scheme where a conservation agency buys credits until a budget constraint is reached. The two options differ when global properties of the cost distribution, such as the mean, change over time. In our simulation, however, costs are in a steady state that is normalized to a mean of 1. Thus, both options are approximately identical except for finite size effects, which would disappear in the limit of an infinitely large landscape. We chose the second option of fixing the budget for the analysis because it allows an easier comparison between different metrics. Appendix B.1 gives a detailed description of the scheduling of the economic model.

### 2.4. Ecological model

To evaluate conservation success in the emerging dynamic landscapes, we use a stochastic metapopulation model (Hanski, 1998; Hanski, 1999). Each conserved grid cell is treated as a habitat patch, meaning that each grid cell may hold a local population of the species. Local populations produce emigrants which may disperse and establish a new local population on an unoccupied cell. At the same time, local populations are subject to local extinction, which may be caused e.g. by demographic or environmental stochasticity. The population as a whole can persist on the landscape if the average recolonization rate is higher than the average local extinction risk, yet, stochastic fluctuations of the number of occupied patches may eventually cause extinction of the whole metapopulation. The better the connectivity among patches, and the more patches in the network, the lower the probability of such a global extinction.

Local extinctions are modelled by a constant chance $e$ of each local population to go extinct per time step. The amount of dispersers arriving from a source patch $x_j$ at a target patch $x_i$ is given by the following dispersal kernel

$$p_{ij} = r \cdot \frac{1}{\sum_i \sigma_i - 1} \cdot e^{-\alpha \cdot d_{ij}}, \tag{5}$$

where $r$ is the emigration rate, the term $(\sum_i \sigma_i - 1)^{-1}$ divides the number of dispersing individuals by the available habitat patches, and the exponential term describes mortality risk during dispersal as a function of distance between $x_i$ and $x_j$. If a patch has been destroyed at the current time step, we set the emigration rate to $r_d$, assuming that a proportion of $r_d$ of the population will be able to disperse before destruction. The sum of all arriving immigrants according to Eq. 5 (truncated to 1) is taken as the probability that this patch is colonized at the current time step. Appendix A gives a detailed description of the scheduling of the ecological model.

### 2.5. Parametrization and analysis of the model

Different species have different connectivity requirements depending on their dispersal abilities. Therefore, we expect an optimized spatial metric to reflect this by values of the connectivity weight $m$ and the connectivity length $l$ that are related to the species characteristics $r, r_d$ and $\alpha$. Additionally, optimal values for $m$ and $l$ may be affected by economic conditions, i.e. the distribution of conservation costs. To analyze the effect of species characteristics and the cost distribution on the optimal spatial incentive, we varied both the connectivity weight $m$ and the connectivity length $l$ of the metric Eq. 1 for three different cost scenarios and for three different species types.

The three cost scenarios were generated by Algorithm 1 at $\Delta = 0.2$, Algorithm 2 at $\Delta = 5 \cdot 10^{-5}$ and $\omega = 0.0065$, and Algorithm 3 at $\Delta = 0.015$ and $\omega = 0.006$. Table 2 displays a summary of the three scenarios. Remember that the first scenario creates uncorrelated costs, the second creates temporally correlated costs and the third scenario creates spatio-temporally correlated costs. Figs. 7 and 8 in Appendix A show the spatial and temporal cost distribution generated by the chosen parameters.

For the species, we consider three functional types: Short-range, intermediate and global dispersers. The parametriza-

**Table 2 – Overview of the cost scenarios created by the three algorithms.**

| COST SCENARIO | PARAMETERS | CHARACTERISTICS |
|---|---|---|
| 1-RANDOM | $\Delta = 0.2$ | uncorrelated |
| 2-RANDOM WALK | $\Delta = 5 \cdot 10^{-5}$<br>$\omega = 0.0065$ | time correlated |
| 3-CORRELATED WALK | $\Delta = 0.015$<br>$\omega = 0.006$ | space and time correlated |

**Table 3 – Parameter values for the three species types considered. $\alpha^{-1}$ is the typical dispersal distance, measured in units of the grid cell length. With cell lengths of 100 m, this translates to typical dispersal distances of 0.5 km, 2.5 km, and 100 km, respectively.**

| SPECIES TYPE | e | r | $r_d$ | $\alpha^{-1}$ |
|---|---|---|---|---|
| I-SHORT DISPERSAL | 0.29 | 3 | 1 | 5 |
| II-INTERMEDIATE DISPERSAL | 0.51 | 3 | 1 | 25 |
| III-GLOBAL DISPERSAL | 0.66 | 3 | 1 | 1000 |

tion for the three species is displayed in Table 3. To assess the extinction risk for the species, we ran the simulation with different random economic starting conditions between 300 and 1000 times and calculated the probability of a metapopulation extinction after 1000 time steps.

The budget constraint $\lambda$ for the aggregated costs (Eq. 4) was fixed at 0.03 times the number of grid cells $n$ for scenarios with cost dynamics generated by the random walk algorithms (economic scenarios 2 and 3) and at 0.05 times the number of grid cells $n$ for the scenarios created with the random algorithm (economic scenario 1). Exceptions are the combination economic scenario 3 with species 3, where aggregated costs were set at 0.1 times $n$ and economic scenario 1 with species 3, where aggregated costs were set at 0.18 times $n$. The adjustment to different budgets was done to create similar survival probabilities across the nine scenarios formed by systematic combination of the three cost scenarios and the three species types.

## 3. Results

### 3.1. Emerging landscapes

For all cost scenarios and all connectivity lengths, an increase in connectivity weight results in more aggregated landscape structures. The density of the clustering is controlled by the connectivity length l, which determines how close patches have to be counted as connected. Smaller connectivity lengths ($l \sim 1.5$, corresponding to the direct eight-cell neighborhood) result in very dense clusters at full connectivity weight, while larger connectivity lengths lead to more loose agglomerations of conserved sites. Due to the spatial cost heterogeneity, there is a trade-off between clustering and area: At a fixed budget, a higher connectivity weight results in lower total area, but with higher clustering. Typical landscapes are displayed in Fig. 3.

### 3.2. Optimal incentive

To find the most effective spatial metric $(m, l)$, we varied connectivity weight between 0 and 1 and connectivity length between 1.5 and 9.5 in 11 linear steps. Note that a conservation market with no spatial trading rules corresponds to a value of $m = 0$. The resulting survival probabilities after 1000 years for the three cost scenarios and the three species types are shown in Fig. 4. The results show that a short disperser such as species I may gain substantially from a very high connectivity weight and short to medium connectivity lengths, while globally dispersing species such as species III benefit from a low connectivity weight and are relatively insensitive towards the connectivity length. For intermediate species such as species II, the tendency changes depending on the cost scenario. An exception is the cost scenario 1 with random costs, which requires very high connectivity weight and short connectivity lengths for all species. We will discuss the reasons for this in the next subsection.

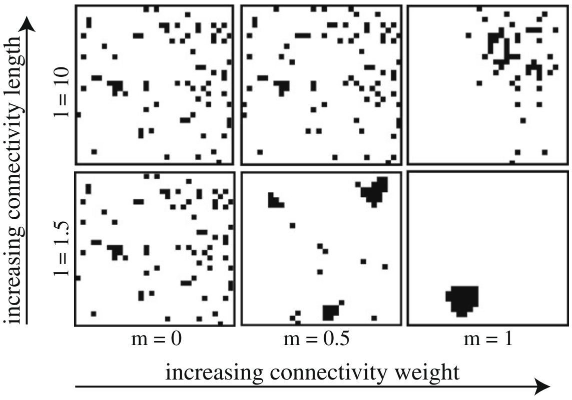


**Fig. 3 – Effect of the connectivity weight *m* and the connectivity length *l*. The pictures show typical landscape structures emerging from trading with costs being sampled by Algorithm 2 at $\Delta = 5 \cdot 10^{-5}, \omega = 0.0065$. Conserved sites are colored black, other sites are colored white. The top row is created with a long connectivity length ($l = 10$), the bottom row with a short connectivity length ($l = 1.5$). The pictures in the left column are taken at $m = 0$, which means that no weight is put on connectivity. Consequently, the landscape structure is dominated by the sites of lowest costs. Increasing connectivity weight ($m = 0.5$ middle, $m = 1$ right) results in increasing clustering of conserved sites, but in a smaller total area. At a connectivity weight of $m = 1$, meaning that all weight is put on connectivity, $l = 1.5$ results in a very dense cluster, while the larger connectivity length $l = 10$ results in a more spread out configuration.**

### 3.3. Interpretation of the results

The observed influence of the cost scenarios on the effectiveness of the applied metric $(m, l)$ suggests that the emerging landscapes differ among the different cost scenarios. To analyze this difference, we plotted landscape connectivity as well as turnover (the fraction of conserved sites that are destroyed and recreated elsewhere per time step) as a function of the metric parameters $m$ and $l$ for the three considered cost scenarios (Fig. 5).

The results show that greater temporal randomness in the costs causes higher turnover, in that landowners switch rapidly between conserving and not conserving. This increase in turnover effectively increases the local extinction risk, because local populations go extinct at the destroyed sites, while the remaining subpopulations can not immediately recolonize the new sites. Creating connected patches leads to more stability, as neighborhood benefits may outweigh

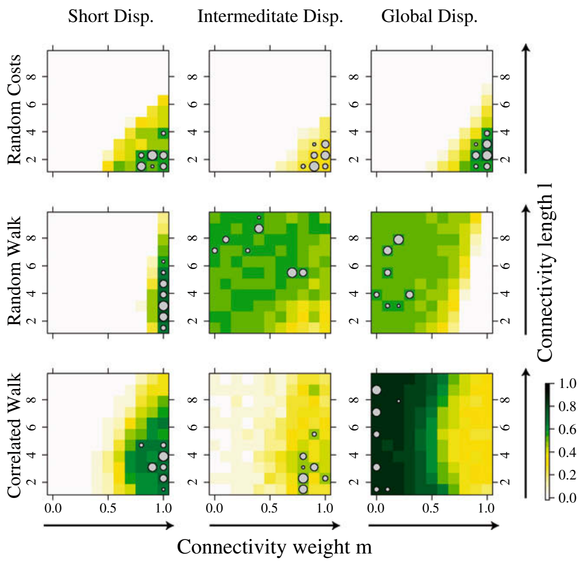


**Fig. 4 – Survival probability as a function of connectivity weight (*x*-axis) and connectivity length (*y*-axis) for the three species types (columns 1–3) and for three cost scenarios (rows 1–3). Dark values represent high survival probabilities. The gray circles mark the seven combinations of $m, l$ that yielded the highest survival probabilities, with larger circle size indicating a better ranking within these seven combinations. For most of the scenarios, these optimal points cluster in one small area of the parameter range. The uncertainty of the survival probability can be estimated from a binomial error model. Typical values of the absolute standard error are in the order of 0.01. This explains why there is some remaining spread of the best combinations of $m, l$ when $m \simeq 0$ is favored (meaning that $l$ has little influence on the model) or when survival probabilities are very similar within a larger area of $(m, l)$.**

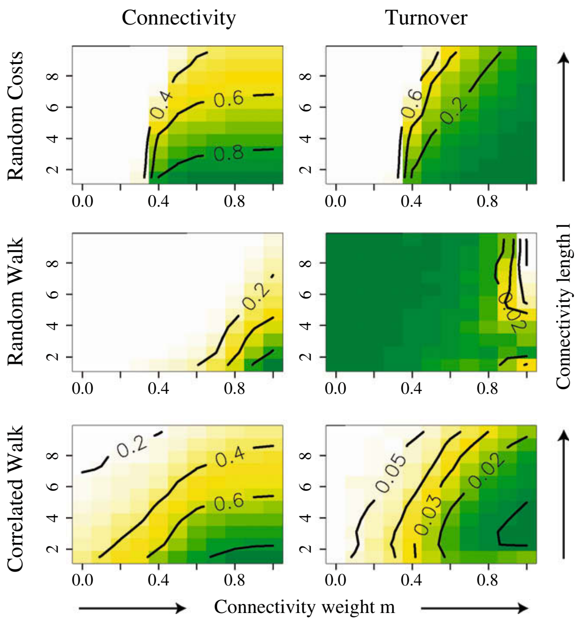


**Fig. 5 – Resulting mean connectivity and turnover for the three cost scenarios as a function of connectivity weight *m* and connectivity length *l*. Connectivity is measured as the mean of $\zeta(1.5)$ of all conserved sites. Turnover, the fraction of conserved sites that are destroyed and recreated elsewhere per time step, serves as an estimate for the intensity of landscape dynamics. Dark values represent low turnover and high connectivity, respectively.**

the individual variation in cost for a cell. Thus we are not only facing a trade-off between area and connectivity, but a trade-off between area, connectivity and turnover. The latter explains why different economic scenarios lead to different optimal metrics: For random costs as in scenario 1, turnover rates are very sensitive to the chosen spatial metric. Consequently, turnover totally dominates species survival and high connectivity weight is favored for all species because it reduces the turnover rate. In contrast, the spatial metric hardly affects turnover for scenarios 2 and 3. Here, the optimization results (Fig. 4) only reflect the trade-off between connectivity and area: Short-range dispersers require high connectivity weights, while global dispersers prefer larger areas.

### 3.4. *Multiple-species optimization*

Assuming that all three species defined in Table 3 share the same habitat, but do not interact, we can also use our model to generate recommendations on how to support all three species at the same time. There are several options available to combine the survival of multiple species into one index (Nicholson and Possingham, 2006; Hartig and Drechsler, 2008b). Here, we use two common indices. The first is the expected number of surviving species, which is given by the sum of the survival probabilities of all species. The second index is the probability of all species surviving, given by the

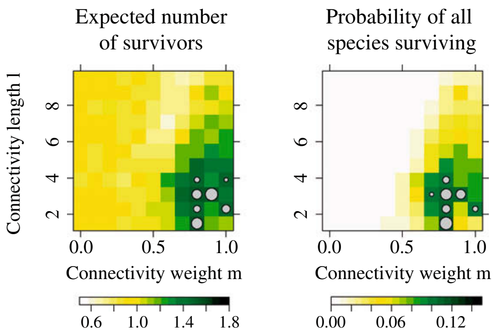


**Fig. 6 – Expected number of surviving species (right) and probabilities of all species surviving (left) for the spatio-temporally correlated costs of scenario 3. The gray circles mark the seven combinations of $m, l$ which yielded the highest score of the applied measure, with larger circle size indicating a better ranking within these seven combinations.**

product of the survival probabilities of all species. As for the single species case, both indices were calculated for a time horizon of 1000 years. Fig. 6 shows the resulting scores for the spatio-temporally correlated cost scenario. Both objectives suggest a moderately strong connectivity weight around $m = 0.8$ and a small connectivity length around 3.

## 4. Discussion

### 4.1. *Main findings*

We presented a coupled ecological–economic model to optimize spatial incentives in a market for conservation credits. The model shows that conservation markets that consider connectivity lead to considerably better conservation results than markets without spatial incentives (represented by $m = 0$ in Fig. 4). Generally, we find that short dispersing species do best with a high weight on connectivity and small-scale connectivity measures. Global dispersers, being largely insensitive to the spatial arrangement of conservation measures, do better with a low weight on connectivity, because this allows the creation of more conserved sites within the given budget. When conserving all species together, a relatively high weight on connectivity yields robustly the highest joint survival probability (Fig. 6). This shows once more that, if connectivity is relevant for the species of concern, spatial evaluation rules may considerably improve the cost-effectiveness of market-based instruments.

Besides species characteristics, the economic scenarios had an additional, and in some cases large, influence on the optimal spatial metric. The reason is that in the presence of dynamic conservation costs, the spatial incentive does not only influence landscape connectivity, but also landscape dynamics (Fig. 5). Landscape dynamics, measured by the rate of turnover (the fraction of conserved sites that are destroyed and recreated elsewhere per time step), negatively affects species survival because the reallocation of a conserved site effectively increases the local extinction risk of the species. In most cases, turnover was negatively correlated with connectivity weight and clustering (Fig. 5). The latter explains why under cost scenario 1 (uncorrelated random costs), a stronger connectivity weight is favored for all species: The spatio-temporally uncorrelated costs of this scenario lead to very high turnover rates under a low connectivity weight. Consequently a high connectivity weight that limits the amount of turnover rates is favored for all species.

### 4.2. *Generality of the results and future research*

The ecological model used for this study neglects a number of factors frequently studied in population models: The landscape is ecologically homogeneous and we have included neither local population dynamics nor a possible dependence of local extinction risk and dispersal on the local population size, nor did we consider correlated environmental stochasticity or catastrophic events. Analyzing the consequences of these factors on the cost-effectiveness of metrics for market-based instruments is a matter of future research. If required all these factors could easily be included without changing the rest of the model, including the analysis method. Furthermore, more sophisticated policies and economic models could be introduced without changing the ecological model.

The main findings of this paper, however, i.e. the positive effect of relatively simple spatial incentives as opposed to no spatial incentives, will qualitatively hold for most realistic scenarios where dispersal is a limiting factor for species. We recommend testing these ideas more often in real-world market schemes such as the examples discussed by (Chomitz et al., 2006) or (Drechsler et al., 2007).

The most apparent shortcoming of the model at this point are simplifications with respect to the time dimension, in particular the inclusion of temporal incentives such as minimum durations of conservation measures on the economic side and time lags for recreation of habitat due to succession on the ecological side. It seems promising for future research to study the control of landscape dynamics through temporal incentives, either independently or in connection with spatial incentives.

### 4.3. *Consequences for conservation policy*

We believe that our results contain three important messages for conservation policy. The first is that the inclusion of spatial incentives may provide a substantial efficiency gain for conservation markets when fragmentation is a crucial factor for the populations under consideration. Our simulations show that it is possible to account for complicated spatial ecological and economic interactions with relatively simple spatial incentives. Given that most existing market-based conservation schemes worldwide do not explicitly account for spatial processes, it seems promising to examine the potential efficiency gains that could be realized by applying spatially explicit metrics for market-based conservation.

The second message is that market-based instruments are likely to produce dynamic landscapes, because a voluntary market is based on the possibility that landowners withdraw from conservation measures while others step in for them. This is not a problem in itself. A moderate amount of landscape dynamics may sometimes even benefit the conservation objective. Yet, landscape dynamics must be considered in the design of marked-based instruments and in underlying ecological models. Neglecting dynamics may lead to severe problems for the ecological effectiveness of a market scheme.

The third message is that optimal spatial incentives are not context-free. The effectiveness of a spatial metric may be sensitive to the economic situation to which it is applied. Thus, a thorough examination of both the ecological as well as the economic and social background is required before deciding on spatial incentives for market-based instruments.

## Acknowledgements

The authors would like to thank Silvia Wissel and Karin Johst for helpful comments during the preparation of the manuscript and Anne Carney for proofreading the text. We are very grateful for the comments which were raised by Doug Bruggeman and two other anonymous reviewers. Their ideas and suggestions greatly contributed to the final manuscript.

## Appendix A. Cost algorithms

Algorithm 1 creates random, spatially, and temporally uncorrelated costs by drawing the costs of each cell for each time step from a uniform distribution of width $2\Delta$. The scheduling within one time step is as follows:

**Algorithm 1.** Random costs

```
for all cells do
    $c_i(t) = random[1 - \Delta \cdots 1 + \Delta]$
end for
```

Algorithm 2 applies a random walk to each grid cell, but has no interaction between grid cells. As a result, we get a temporal correlation of the costs of each grid cell (Fig. 8), but a spatially random pattern (Fig. 7). To constrain the random walk around 1, an additional rebounding factor of $\omega \cdot \sqrt{|1 - c_i(t-1)|}$ was added to the random walk. The scheduling within one time step is as follows:

**Algorithm 2.** Random Walk

```
for all cells do
    $c_i(t) = c_i(t-1) + \Delta \cdot random[-1 \cdots 1] +$
    $\omega \cdot sign(1 - c_i(t-1)) \cdot \sqrt{|1 - c_i(t-1)|}$
end for
```

Algorithm 3 applies a random walk with an additional spatial interaction to each grid cell. It produces spatio-temporally correlated costs (Figs. 7 and 8). The scheduling within one time step is as follows:

**Algorithm 3.** Correlated random walk

```
Calculate average global costs
for all cells do
    $\bar{c}_i$ = average costs in the eight-cell neighborhood
    $c_i(t) = c_i(t-1) + \Delta \cdot random[-1 \cdots 1] + \omega \cdot \bar{c}_i$
Normalize with average global costs
end for
```

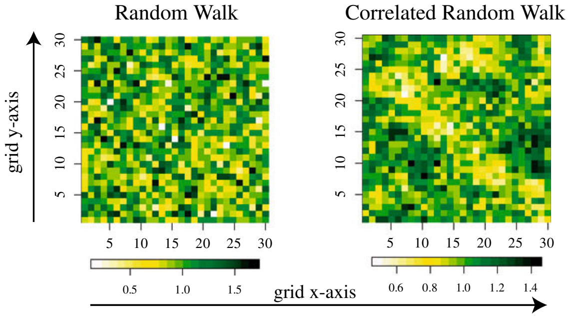
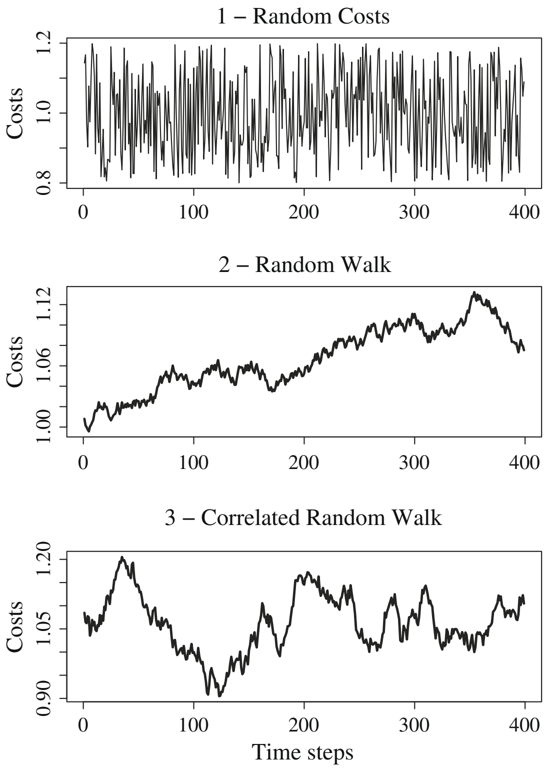


**Fig. 7 – Spatial cost distributions generated by the random walk algorithms (Algorithms 2 and 3). The two figures show the 30 × 30 grid cells with high cost cells in light and low cost cells in dark colors. The left figure was created by the random walk (Algorithm 2) at $\Delta = 5 \cdot 10^{-5}, \omega = 0.0065$, to the right the correlated random walk (Algorithm 3) at $\Delta = 0.015, \omega = 0.006$. Note that low and high cost areas are clustered for the correlated random walk.**


1 – Random Costs

2 – Random Walk

3 – Correlated Random Walk

**Fig. 8 – Time series of the costs of a grid cell over time. Algorithm 1 which changes costs randomly at each time step creates a strongly fluctuating time series. The two random walk algorithms lead to a time-correlated series.**

## Appendix B. Model scheduling

### B.1. *Economic model*

The economic model is initialized with a random configuration which is at the desired cost level. To ensure that the random walks are in a steady state, we ran the simulation 10,000 time steps before the ecological model was initialized. Each time step, the scheduling was as follows:

**Algorithm 4.** Scheduling economic model

```
Update costs
repeat
    Adjust market price
    for all cells do
        if $P \cdot \xi_i(I) > c_i(t)$ then
            $x_i = 1$ (conserved)
        else
            $x_i = 0$ (not conserved)
        end if
    end for
    Calculate ecological value and costs
until budget constraint is met
Update land configuration
```

### B.2. *Ecological model*

The ecological model was started by randomly choosing 60% of the patches as occupied. We checked that populations were in a steady state after initialization and thus the measurements were not affected by the initialization [Grimm and Wissel, 2004, see]. The scheduling of the ecological model within one time step is as follows:

**Algorithm 5.** Scheduling metapopulation model

```
for all populated cells do
  Local extinction with rate $e$
end for
for all populated cells do
  if Patch destroyed then
    Disperse with emigration rate $r_d$
  else
    Disperse with emigration rate $r$
  end if
end for
for all unpopulated cells do
  Check if immigration succesfull
end for
```

## REFERENCES

Ando, A., Camm, J., Polasky, S., Solow, A., 1998. Species distributions land values and efficient conservation. Science 279 (5359), 2126–2128. doi:10.1126/science.279.5359.2126.

Bruggeman, D., Jones, M., 2008. Should habitat trading be based on mitigation ratios derived from landscape indices? A model-based analysis of compensatory restoration options for the red-cockaded woodpecker. Environmental Management 42 (4), 591–602. doi:10.1007/s00267-008-9179-2.

Chomitz, K.M., 2004. Transferable development rights and forest protection: an exploratory analysis. International Regional Science Review 27 (3), 348–373. doi:10.1177/0160017604266030.

Chomitz, K.M., da Fonseca, G.A.B., Alger, K., Stoms, D.M., Honzak, M., Landau, E.C., Thomas, T.S., Thomas, W.W., Davis, F., 2006. Viable reserve networks arise from individual landholder responses to conservation incentives. Ecology and Society 11 (2), 40.

Coggan, A., Whitten, S.M., 2005. Market based instruments (MBIs) in Australia: What are they, important issues to consider and some applications to date. Tech. rep., CSIRO. http://www.ecosystemservicesproject.org/html/publications/docs/Intro_to_MBIs_2005.pdf (accessed 29.11.2008).

Drechsler, M. Wätzold, F., in press. Applying tradable permits to biodiversity conservation: effects of space-dependent conservation benefits and cost heterogeneity on habitat allocation. Ecological Economics. doi: 10.1016/j.ecolecon.2008.07.019.

Drechsler, M., Wätzold, F., Johst, K., Bergmann, H., Settele, J., 2007. A model-based approach for designing cost-effective compensation payments for conservation of endangered species in real landscapes. Biological Conservation 140 (1-2), 174–186. doi:10.1016/j.biocon.2007.08.013.

EU-Commission, 2007. Green paper on market-based instruments for environment and related policy purposes. Tech. rep., Commission of the European Communities. http://eur-lex.europa.eu/LexUriServ/site/en/com/2007/com2007_0140en01.pdf (accessed 29.11.2008).

Fahrig, L., 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. Ecological Applications 12 (2), 346–353.

Ferraro, P.J., Kiss, A., 2002. Direct payments to conserve biodiversity. Science 298 (5599), 1718–1719. doi:10.1126/science.1078104.

Ferraro, P.J., Pattanayak, S.K., 2006. Money for nothing? A call for empirical evaluation of biodiversity conservation investments. PLoS Biology 4 (4), E105. doi:10.1371/journal.pbio.0040105.

Fox, J., Nino-Murcia, A., 2005. Status of species conservation banking in the United States. Conservation Biology 19 (4), 996–1007. doi:10.1111/j.1523-1739.2005.00231.x.

Grimm, V., Wissel, C., 2004. The intrinsic mean time to extinction: a unifying approach to analysing persistence and viability of populations. Oikos 105 (3), 501–511. doi:10.1111/j.0030-1299.2004.12606.x.

Hanski, I., 1998. Metapopulation dynamics. Nature 396, 41–49. doi:10.1038/23876.

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

Hanski, I., Moilanen, A., Gyllenberg, M., 1996. Minimum viable metapopulation size. American Naturalist 147 (4), 527–541.

Hartig, F., Drechsler, M., 2008a. Stay by thy neighbor? Structure formation, coordination and costs in tradable permit markets with spatial trading rules. arXiv:0808.0111v1. http://arxiv.org/abs/0808.0111v1.

Hartig, F., Drechsler, M., 2008b. The time horizon and its role in multiple species conservation planning. Biological Conservation 141 (10), 2625–2631. doi:10.1016/j.biocon.2008.07.028.

Jack, B.K., Kousky, C., Sims, K.R.E., 2008. Designing payments for ecosystem services: lessons from previous experience with incentive-based mechanisms. Proceedings of the National Academy of Sciences 105 (28), 9465–9470. doi:10.1073/pnas.0705503104.

Latacz-Lohmann, U., Schilizzi, S., 2005. Auctions for conservation contracts: a review of the theoretical and empirical literature. Tech. rep., Report to the Scottish Executive Environment and Rural Affairs Department. http://www.scotland.gov.uk/Publications/2006/02/21152441/0.

Latacz-Lohmann, U., Van der Hamsvoort, C.P.C.M., 1998. Auctions as a means of creating a market for public goods from agriculture. Journal of Agricultural Economics 49 (3), 334–345.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405 (6783), 243–253. doi:10.1038/35012251.

Mills, D.E., 1980. Transferable development rights markets. Journal of Urban Economics 7 (1), 63–74. doi:10.1016/0094-1190(80)90026-1.

Moilanen, A., 2005. Reserve selection using nonlinear species distribution models. American Naturalist 165 (6), 695–706. doi:10.1086/430011.

Nelson, E., Polasky, S., Lewis, D.J., Plantinga, A.J., Lonsdorf, E., White, D., Bael, D., Lawler, J.J., 2008. Efficiency of incentives to jointly increase carbon sequestration and species conservation on a landscape. Proceedings of the National Academy of Sciences of the United States of America 105 (28), 9471–9476. doi:10.1073/pnas.0706178105.

Nicholson, E., Possingham, H.P., 2006. Objectives for multiple-species conservation planning. Conservation Biology 20 (3), 871–881. doi:10.1111/j.1523-1739.2006.00369.x.

Panayotou, T., 1994. Conservation of biodiversity and economic development: the concept of transferable development rights. Environmental & Resource Economics 4 (1), 91–110. doi:10.1007/BF00691934.

Polasky, S., Nelson, E., Camm, J., Csuti, B., Fackler, P., Lonsdorf, E., Montgomery, C., White, D., Arthur, J., Garber-Yonts, B., Haight, R., Kagan, J., Starfield, A., Tobalske, C., 2008. Where to put things? Spatial land management to sustain biodiversity and economic returns. Biological Conservation 141 (6), 1505–1524. doi:10.1016/j.biocon.2008.03.022.

Salzman, J., Ruhl, J.B., 2000. Currencies and the commodification of environmental law. Stanford Law Review 53 (3), 607–694.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5 (1), 18–32. doi:10.1111/j.1523-1739.1991.tb00384.x.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413 (6856), 591–596. doi:10.1038/35098000.

van Teeffelen, A., Cabeza, M., Moilanen, A., 2006. Connectivity probabilities and persistence: comparing reserve selection strategies. Biodiversity and Conservation 15 (3), 899–919. doi:10.1007/s10531-004-2933-8.

Wilcove, D.S., Lee, J., 2004. Using economic and regulatory incentives to restore endangered species: lessons learned from three new programs. Conservation Biology 18 (3), 639–645.

Williams, P.H., Araujo, M.B., 2000. Using probability of persistence to identify important areas for biodiversity conservation. Proceedings of the Royal Society of London Series B-Biological Sciences 267 (1456), 1959–1966. doi:10.1098/rspb.2000.1236.

Wunder, S., 2007. The efficiency of payments for environmental services in tropical conservation. Conservation Biology 21 (1), 48–58. doi:10.1111/j.1523-1739.2006.00559.x.

paper III

Florian Hartig, Martin Horn, Martin Drechsler

# EcoTRADE - a multi-player network game of a tradable permit market for biodiversity credits

**Environmental Modelling and Software, in press**
**doi: 10.1016/j.envsoft.2009.01.003**
**repository: arxiv.org/abs/0812.0956**

**Summary:** We introduce a multi-player network game which may be used to analyze the strategies of players when faced with spatial conservation incentives.

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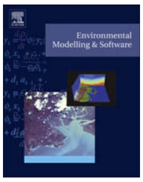

Software, Data and Modelling News

# EcoTRADE – A multi-player network game of a tradable permit market for biodiversity credits

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ABSTRACT

EcoTRADE is a multi-player network game of a virtual biodiversity credit market. Each player controls the land use of a certain amount of parcels on a virtual landscape. The biodiversity credits of a particular parcel depend on neighboring parcels, which may be owned by other players. The game can be used to study the strategies of players in experiments or classroom games and as a communication tool for stakeholders participating in credit markets that include spatially interdependent credits.

## Software availability

Name of the software: EcoTRADE
Availability: Software, documentation and an online applet are available at http://www.ecotrade.ufz.de/ecotradegame.
Developers: Martin Horn, Martin Drechsler, Florian Hartig
Year first available: 2008
Software required: Java (JRE version 1.5 and higher). Additionally, the web browser must allow the execution of java applets for an optional online view.
Programming language: Java

## 1. Introduction

Tradable permits are an economic instrument for controlling the use of environmental resources. Examples of tradable permits include the carbon emissions trading schemes settled under the Kyoto Protocol or the tradable permit system for restricting emissions of ozone-depleting chemicals in the US after 1988 (Tietenberg, 2006). In recent years, tradable permit schemes with names such as biobanking or biodiversity credit trading have also been applied to restrict land use and ensure the maintenance of natural habitats and biodiversity (Wissel and Wätzold, 2008). Yet, unlike in the case of carbon emissions, biodiversity credits cannot be issued independently of the spatial location. Species depend on the connectedness of their habitat. Therefore, the ecological benefit of conserving a site is higher in the vicinity of other conserved sites and credits should be issued accordingly (Drechsler and Wätzold, in press; Hartig and Drechsler, in press).

The multi-player game EcoTRADE illustrates such a situation: In a virtual biodiversity credit market, players may use their land for conservation or agricultural purposes. The amount of biodiversity credits they receive depends on the land use in their neighborhood. Players interact through these neighborhood-dependent benefits and by trading credits on a virtual market. The software may be used for educational purposes, such as classroom experiments, as well as for communication with stakeholders or for experimental economics.

## 2. Game description and software features

At the beginning of the game, each player receives a certain land entitlement and a certain conservation obligation. To produce more or less biodiversity credits, players can change the land use type of a parcel through mouse clicks. If players want to undersupply their obligation, they first need to buy credits from other players. An overplus of credits can be sold to other players. The aim of the game

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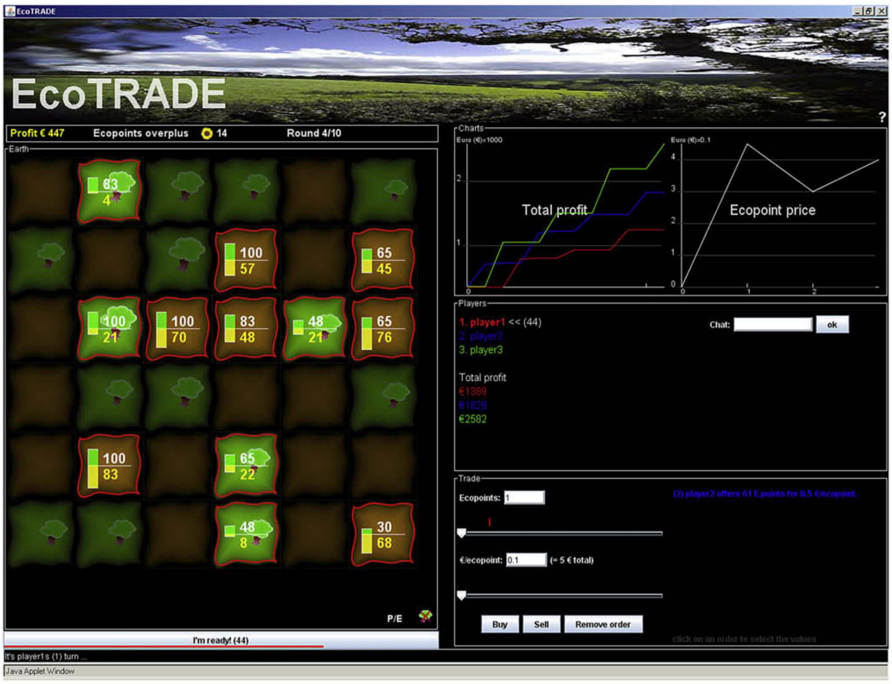

Profit € 447 Ecopoints overplus 14 Round 4/10

1. player1 << (44)
2. player2
3. player3

Total profit
€1389
€1829
€2582

Ecopoints: 1

€/ecopoint: 0.1 (= 5 € total)

(2) player2 offers 61 E.points for 0.5 €/ecopoint.

click on an order to select the values

It's player1's (1) turn

**Fig. 1.** A three-player game, showing the client window of player 1. On the left hand side we see the game landscape. Properties belonging to player 1 are highlighted. Each of these properties is labelled with two numbers; the upper one denotes the conservation credits earned from the property if used for conservation, the lower one marks the economic profit earned from the property if used for agriculture. A tree on a property indicates that the site is used for conservation. On the right hand side (from top to bottom), we see the current profits of all players and the time series of prices of ecopoint transactions (top); status information and a chat window (middle); and a window for credit trading (bottom).

is to maximize economic profits from the land, which can be done by collecting revenue from agriculturally used fields or by selling biodiversity credits to other players (see Fig. 1).

The software consists of a server and a client. The clients, controlled by the players, may connect to the server through any network connection, i.e. via a local network or the Internet. Players may initialize new games on the server, modify the rules of the new game, and invite other players to join in. All parts of the software are written in Java and can be run on any system which provides a java virtual machine. User manuals in English and German can be found on the game website, from where it is also possible to play the game directly in the web browser. The software also contains an experimental one-player version, where the second player is controlled by the computer.

## 3. Practical experience and concluding remarks

Credit markets with spatially dependent credits give rise to a number of questions. Landowners may influence each other's payoffs (see Hartig and Drechsler, submitted for publication). Will they coordinate or cooperate to optimize their profits? Will they be able to find the land configurations that optimize their payoffs? Will players find it unfair that other players may influence their payoffs?

The EcoTRADE software has been used at several workshops with participants ranging from children between the ages of 10 and 15 years to ecology and economics students and scientists working in the field of conservation and resource economics. We found that the software is useful for observing the typical behavior and strategies of players, but also for communicating problems arising from spatially interdependent credits. In conclusion, we hope that users will find the EcoTRADE game useful as a communication tool for classroom games and stakeholder workshops, but also for experimental studies in economics.

## References

Drechsler, M., Wätzold, F. Applying tradable permits to biodiversity conservation: effects of space-dependent conservation benefits and cost heterogeneity on habitat allocation. Ecological Economics (2008), doi: 10.1016/j.ecolecon.2008.07.019, in press.

Hartig, F., Drechsler, M. Smart spatial incentives for market-based conservation. Biological Conservation (2009), doi: 10.1016/j.biocon.2008.12.014, in press.

Hartig, F., Drechsler, M. Stay by thy neighbor? Structure formation, coordination and costs in tradable permit markets with spatial trading rules, http://arxiv.org/abs/0808.0111, submitted for publication.

Tietenberg, T., 2006. Emissions Trading Principles and Practice, second ed. RFF Press.

Wissel, S., Wätzold, F., 2008. Applying tradable permits to biodiversity conservation: a conceptual analysis of trading rules. UFZ Discussion Paper 7/2008.

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paper IV

Florian Hartig, Martin Drechsler

# Stay by thy neighbor? Social organization determines the efficiency of biodiversity markets with spatial incentives

**Ecological Complexity, in press**
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**repository: arxiv.org/abs/0808.0111**

**Summary:** We show that, when market values of conservation measures interact, both the distribution of interactions benefits between landowners and the social organization of landowners affect the effectiveness of the conservation policy.

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# Stay by thy neighbor? Social organization determines the efficiency of biodiversity markets with spatial incentives

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ABSTRACT

Market-based conservation instruments, such as payments, auctions or tradable permits, are environmental policies that create financial incentives for landowners to engage in voluntary conservation on their land. But what if ecological processes operate across property boundaries and land use decisions on one property influence ecosystem functions on neighboring sites? This paper examines how to account for such spatial externalities when designing market-based conservation instruments. We use an agent-based model to analyze different spatial metrics and their implications on land use decisions in a dynamic cost environment. The model contains a number of alternative submodels which differ in incentive design and social interactions of agents, the latter including coordinating as well as cooperating behavior of agents. We find that incentive design and social interactions have a strong influence on the spatial allocation and the costs of the conservation market.

## 1. Introduction

What is the value of nature? Markets for biodiversity conservation are based on the possibility of rating conservation services (e.g. the provision of an acre of rainforest) in terms of their contribution to conservation goals. A problem that arises when deciding on rating systems is that typical ecological processes operate on a much larger scale than that of typical landowner properties. Therefore, local land use decisions are likely to affect the ecological value of neighboring land. This paper deals with the problem of incorporating such spatial interactions into market-based conservation instruments.

Market-based instruments have become increasingly popular in recent years (Jack et al., 2008), however, they are still a relative new tool for conservation policy. Traditionally, conservation was dominated by regulation and planning approaches which emerged as a response to problems associated with the change and intensification of land use during the last century. Of particular importance for the effectiveness of top-down approaches such as regulations and planning is the inclusion of both the monetary costs and the ecological benefits of conservation measures (Faith and Walker, 1996; Ando et al., 1998; Margules and Pressey, 2000). This insight points to a practical problem of planning approaches: local costs are difficult or expensive to estimate, and it is seldom in the interest of landowners to report them honestly. Moreover, costs may change over time. In these cases, market instruments provide an alternative to planning approaches because they are able to efficiently allocate conservation efforts to the spatial distribution of conservation costs, even when cost information is only available to landowners and not to the regulating authorities (information asymmetry).

The common principle of market-based instruments is to introduce a metric that rates the value of conservation measures in terms of their contribution to conservation goals. This metric translates conservation measures into one currency (commodification) and thereby makes conservation comparable and tradable based on this currency (Salzman and Ruhl, 2000; Salzman, 2005). In practice, different names are used for this currency. We will use the term “credits” throughout this paper, and say that the metric measures the amount of conservation provided by a site in credits.

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Demand for credits may be created by different mechanisms, e.g. payments (Wunder, 2007; Drechsler et al., 2007; Engel et al., 2008), auctions (Latacz-Lohmann and Van der Hamsvoort, 1998) or biodiversity offset schemes (Panayotou, 1994; Chomitz, 2004). This demand for credits, together with the metric to measure them, creates an incentive for conservation. In a sense, we may view the process of trading credits as a policy-based site selection algorithm (Faith et al., 2003): competition among suppliers automatically extracts the sites that can provide conservation measures at the lowest costs.

Yet, while markets may help to solve the problem of cost information asymmetry between landowners and regulators, the definition of an accurate measure of conservational value runs into problems when the ecological values of sites are dependent on each other. An apparent solution is to incorporate spatial dependencies into market values (Parkhurst et al., 2002). While this is generally possible, it implies that conservation decisions may change the market value of neighboring land. In the presence of such spatial interactions, referred to in the literature as externalities, spillovers or site synergies, markets may fail to create an efficient spatial allocation of the traded good (Mills, 1980). Moreover, ecological processes may operate on a large range of spatial and temporal scales and show complex dependencies, making the exact accounting for ecological interactions potentially very difficult. Moilanen (2005) discusses a case of interactions where already static optimization is computationally hard. In such a case, it is unlikely that market participants would find the optimal allocation of conservation measures, particularly if they are subject to external drivers such as changing conservation costs.

The aim of this paper is to analyze the functioning of simple spatial incentives in market-based conservation instruments. We use an agent-based model to examine whether simple spatial connectivity incentives operating on a local scale can effectively influence the larger scale allocation of conservation measures, and how design of the spatial incentives and social organization affect the emerging landscape structure.

## 2. Problem definition and modeling approach

The fact that sites may interact and influence the ecological value of neighboring sites creates a number of issues which make spatial incentives an interesting problem for economics and conservation research. A number of important real-world processes create spatial interactions between sites. One example is habitat fragmentation, which constitutes a major problem for biodiversity conservation (Saunders et al., 1991; Ma, 2005). The origin of this problem is that many species require to travel between habitat patches in the landscape. When habitats are increasingly isolated, e.g. through land use change, they may eventually be of very low value for biodiversity because species cannot reach them. Therefore, the ecological value of a natural habitat generally increases when other natural habitats are in the vicinity.

In this paper, we assume that there is a symmetric, positive interaction benefit between conserved sites. As discussed above, this is very likely to be the case in real-world conservation problems. However, other cases such as non-symmetric benefits (see Vuilleumier and Possingham, 2006) or negative interactions could equally be targeted with markets. The aim of this section is to clarify the conceptual questions that arise from including spatial incentives in market instruments, and to formulate more precisely the questions we want to answer with the model.

### 2.1. Marginal and additive incentives

The first question relates to the difference between the total and the local valuation of conservation measures. Let us assume that we have a market instrument with spatial incentives, and we have a metric $U$ which measures the ecological value of a landscape and includes spatial interactions between sites. As an example, we may have two sites which have, as isolated sites, an ecological value of 2 credits each. If each site benefits from the presence of the other, the total ecological value of the two sites will be higher than the sum of the single sites, which is $2 + 2 = 4$ credits. Let us assume that the collective value $U$ is 6 credits, consisting of the single values which amounted to 4 credits, and 2 additional credits originating from the positive interactions. What is the value of these connected sites? One may assume that, as both sites are identical, it should be 3 for each site. However, removing any of the two connected sites would leave us with a single site of value 2, suggesting that the value of the first site which was removed was in fact 4. An illustration of this is given in Fig. 1.

To give a more mathematical description of this, assume that the metric measuring the credits awarded to a site is as follows:

$$U = \sum_i \{(1-m)A_i + m\beta_i\}. \tag{1}$$

Here, the sum runs over all conserved sites, and each site is evaluated according to its area $A_i$ and its connectivity $\beta_i$, i.e. its connection and therefore its interactions with neighboring sites. For now, we view $\beta_i$ as a generic measure of connectivity, but we will give a specific expression in the model description. The parameter $m$, taking values from 0 to 1, specifies the trade-off between area $A_i$ and connectivity $\beta_i$. We call $m$ the connectivity weight. If $m = 0$, a connected site receives the same amount of credits as an unconnected site. Increasing $m$, connectivity becomes more important. If $m = 1$, only the connectivity of sites is rewarded with credits. Despite its simplicity, this function essentially captures the trade-off between area and connectivity, which is found to be very important for the conservational value of sites in fragmented landscapes (e.g. Frank and Wissel, 2002; Drechsler, 2009). The appropriate value of $m$ depends on the species under consideration. For some systems, connectivity is more important, while others depend mostly on area.

**Marginal incentives** (1): The change of total ecological value originating from the removal of one site is called the marginal value $b^{mar}$ of this site. For our former example, each of the two connected sites has a marginal value of 4, because their removal would decrease the total value $U$ by 4. Assuming Eq. (1), the marginal value of the $i$th site is given by

$$b_i^{mar} = (1-m)A_i + 2m\beta_i \tag{2}$$

The factor 2 in the second term originates from the fact that not only the connectivity of the focal site is removed, but also the connectivity of the sites it interacts with is decreased by the same value (symmetric benefits). Incentives based on the marginal value we call "marginal incentives". There are two important points to note about marginal incentives. Firstly, if more than one site is changed, the marginal values of the sites depend on the order of trading. Assuming a positive interaction between sites, there is a first-mover disadvantage: the marginal value of the first site created is less than the marginal value of the second site, and the costs for the first site to be removed are higher than for the second site (Fig. 1). Secondly, the marginal value of two sites is generally not the sum of the two sites' marginal values. Marginal values do not add up to the total value. These two properties have strong implications for conservation policy. For using marginal incentives, we have to make sure that the order of trading is known, i.e. that trading takes place sequentially. Moreover, another problem arises when landowners want to withdraw a site from the market, and this sites marginal value has changed since creation because other sites have been added in the vicinity. Marginal incentives require

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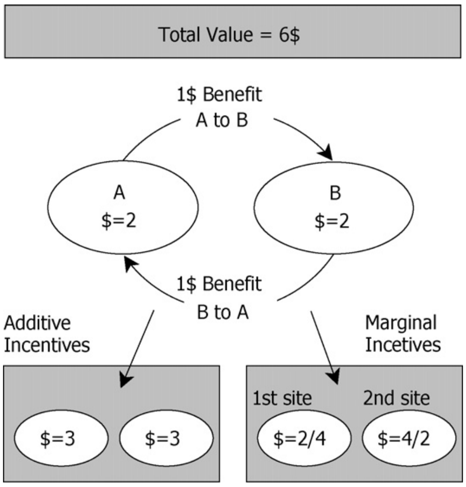

**Fig. 1.** Two sites of equal size, A and B, are of mutual benefit to each other. When isolated, each site has an ecological value of 2 each. Connecting the two sites creates an additional value of 2, the results of a benefit of 1 in each direction. Given additive incentives, each landowner receives 3 credits, while under marginal incentives, the first one to come would receive 2 credits, whilst the second receives 4 credits because his site adds all the mutual benefits and thus confers a marginal value of 4 to the network. Yet, note that if both sites are present, each site has a marginal value of 4. Therefore, the first site to be removed would create a marginal damage of 4, while the damage of removing the second site would only be 2, as indicated by the second number.

that the costs for withdrawing such a site must be higher than the benefits initially awarded for it (see Fig. 1). This means that marginal incentives are difficult to use for short term incentive mechanisms such as yearly payments. They are, however, very suitable for markets such as tradable permits where both creation and destruction is targeted, or markets with long-term contracts, where the problem of habitat destruction does not arise.

**Additive incentives** (2): Another way to arrive at a sensible local evaluation of sites is by simply dividing mutual benefits equally among the involved sites (see Fig. 1). The value that results from sharing the benefits is still higher than the value of isolated sites, but it is generally lower than the marginal value. For the case of Eq. (1), equally sharing the mutual benefits results in local values of

$$b_i^{add} = (1-m)A_i + m\beta_i \quad (3)$$

We call these incentives additive incentives because their sum adds up to the total value:

$$\sum_i b_i^{add} = U. \quad (4)$$

Markets with additive spatial incentives have been suggested, e.g. by Parkhurst et al. (2002) or Hartig and Drechsler (2009), as a means to improve the spatial agglomeration of conservation sites. Additive incentives have the advantage that the order of creation or destruction has no impact on the value of a particular site, and the value of any number of sites is simply the sum of the values of these sites. One drawback, however, is that a change of conservation on one site may directly affect the ecological value and therefore the credits awarded to neighboring conserved sites. This might create acceptance problems for real-world conservation schemes. Another issue is that marginal values assign only a part of the costs and benefits created by a land use change to its originator. This may lead to efficiency losses. We show evidence for this in the results.

### 2.2. Social organization

If market incentives for conserving a site depend on the neighboring sites, it is important for landowners to know their neighbors' intentions. We assume that agents are always profit maximizing and myopic in the sense that they base their decision on the most profitable action for the next timestep without displaying strategic behavior. Within this setting, we consider three behavioral submodels:

**Null model** (a): In the null model, agents observe the present landscape configuration and decide based on the prospect of the future land configuration being the same as the present one.

**Coordination through cheap talk** (b): We assume that agents may communicate their future intentions. This can be beneficial because it increases the accuracy of the estimate about the upcoming land configuration. We understand coordination as the communication of non-binding information about the present state of the decision, often called cheap talk (Farrell and Rabin, 1996). Experimental studies have shown that the possibility of coordination by cheap talk leads to an increased probability of finding cost-effective configurations (Parkhurst et al., 2002). Generally, cheap talk also includes the possibility of strategic lies. This option is omitted in the simulation and hence agents will always stick to the action they communicated as long as their information does not change.

**Cooperation** (c): Further payoff improvements are possible if agents not only coordinate, but cooperate. Cooperation means that conservation is provided if it is beneficial for the group, even if this does not maximize the profits of each individual. As marginal and additive incentives differ only in how benefits are distributed to individuals, but not in how many credits are rewarded in total, there is no difference between them from the point of view of cooperating agents. In a cooperating group, agents reveal their true costs, the group chooses the best configuration of sites, and the payoffs are distributed among the group members according to their costs. It would be possible that single individuals exploit such a system by communicating higher than the true costs to increase their share from the group benefits. We do not consider this possibility in the model, but we will address this issue in the discussion.

For options (a) and (b), decisions are made individually, while cooperating agents (c) decide collectively. We will later see that these structurally different decision processes are also reflected in the resulting land use pattern. Table 1 summarizes the possible combinations of submodels and their properties.

## 3. Model description

### 3.1. Overview and purpose

The aim of the model is to examine the effect of spatial incentives and social organization on the emerging landscape structures and on the total cost of a conservation market. The model is based on the models introduced in Drechsler and Wätzold (2009) and Hartig and Drechsler (2009). It predicts the spatial allocation of conservation sites emerging from agents' decisions to conserve their land or not. These decisions are driven by spatially and temporally heterogeneous costs of conservation and by the benefits of conservation, which depend on the current market price and on the amount of conserved cells in the neighborhood. This dependence on the state of the neighboring cells resembles 2-dimensional spin models with local interactions which have been used to analyze phenomena of social interactions (Galam and Zucker, 2000; Sznajd-Weron and Sznajd, 2000; Holyst et al., 2000; Schweitzer et al., 2002). It also exhibits similarities to the Random Field Ising Model (Imry and Ma, 1975) and non-equilibrium

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**Table 1**
Overview of alternative submodels for the spatial incentives and for agent behavior.

| Label | Submodel | Decisions | Time order | Communication |
|---|---|---|---|---|
| (a.1) | Null marginal | Individually | Dependent | None |
| (a.2) | Null additive | | Independent | |
| (b.1) | Coordination marginal | | Dependent | Intentions |
| (b.2) | Coordination additive | | Independent | |
| (c) | Cooperation | Collectively | Independent | Full information |

models such as Hausmann and Rujan (1997) and Acharyya (1998). In the follwowing subsections, we give an overview first of state variables and scales, and then about the processes implemented in the model.

### 3.2. State variables and scales

The simulation is carried out on a 2-dimensional grid with $50 \times 50$ grid cells (sites) and periodic boundary conditions. Every grid cell $x_i$ is owned by a different landowner (agent) and can be occupied with a habitat ($\sigma_i = 1$) or be used for other purposes ($\sigma_i = 0$). Although the model may be applied to any spatial and temporal scale, we think of grid cells as being of the size of an average agricultural field in Europe, and time steps being a year. The occupancy of a grid cell results in conservation costs $c_i(t)$ which may be different for each cell.

We assume that we have a market instrument which rewards a certain price $P$ for each conservation credit produced by landowners. Conservation credits are calculated according to the metric given in Eq. (1), where the area $A_i$ was set to unity and is therefore omitted.

$$U = \sum_{i}^{N} \sigma_i \{(1-m) + \ m\beta_i\}. \tag{5}$$

As before, $m$ weights the importance of connectivity $\beta_i$ relative to area for the ecosystem function which is targeted by the market. The connectivity metric $\beta_i$, which measures the interactions between patches, is chosen as

$$\beta_i \equiv \frac{1}{8} \sum_{\langle j \rangle_i} \sigma_j, \tag{6}$$

where $\langle j \rangle_i$ indicates all cells $j$ which belong to the 8 cells $x_j$ in a Moore neighborhood of $x_i$. The metric is normalized to one and basically measures the fraction of the 8 cells in the neighborhood of the focal cell which are used for conservation. We assume a totally inelastic demand

$$D = \lambda N \tag{7}$$

for conservation credits, which should equal the supply $U$. A list of all basic state variables and parameters is given in Table 2. We define the average number of occupied sites

$$\alpha \equiv \frac{1}{N} \sum_{i=1}^{N} \sigma_i. \tag{8}$$

**Table 2**
List of state variables (top) and parameters (bottom).

| Symbol | Connotation | Range |
|---|---|---|
| $x_i$ | $i$th cell on the grid | |
| $\sigma_i$ | State of the $i$th cell | $\{0, 1\}$ |
| $c_i(t)$ | Costs of $\sigma_i = 1$ at t | $[1-\delta \ldots 1+\delta]$ |
| $P$ | Market price | $[1-\delta \ldots 1+\delta]$ |
| $\delta$ | Cost heterogeneity | $[0 \ldots 1]$ |
| $m$ | Connectivity weight | $[0 \ldots 1]$ |
| $\lambda$ | Fixed demand | $[0 \ldots 1]$ |

Further, we define the average connectivity $K$ of the occupied sites as

$$K \equiv \frac{1}{\alpha N} \sum_{i=1}^{N} \sigma_i \beta_i \tag{9}$$

and total conservation costs $C$ of a landscape configuration as the sum of the costs of all conserved grid cells, divided by the number of grid cells

$$C \equiv \frac{1}{N} \sum_{i=1}^{N} \sigma_i c_i. \tag{10}$$

### 3.3. Process overview and scheduling:

At each time step, costs $c_i$ are drawn from a uniform distribution of mean 1 and width $2\delta$. Agents decide to maintain a site as habitat based on their costs $c_i$, the market price $P$ and the estimated credit value $\tilde{b_i}$. They maintain a habitat on $x_i$ at timestep $t$ if conservation yields a positive net benefit $\pi$

$$\pi_i \equiv -c_i(t) + P\tilde{b_i}(t) > 0. \tag{11}$$

The credits rewarded to agents are either the marginal incentives (Eq. (2)) given by $(1-m) + 2m\beta$ or the additive incentives (Eq. (3)) given by $(1-m) + m\beta$. The final benefits $b_i$ rewarded at the end of the round can differ from the estimated benefits $\tilde{b_i}$ because subsequent decisions by other agents can change the landscape configuration. The accuracy of the estimate $\tilde{b_i}$ depends on the applied behavior submodel. The three submodels discussed in Section 2.2 are implemented in the following way:

**Null model**: All agents decide in parallel according to Eq. (11) without being informed about the decisions of other agents at this timestep.

**Coordination through cheap talk**: Agents decide sequentially in random order according to Eq. (11). After each decision, all agents are informed about the new configuration. This procedure is repeated a number of times, mimicking the outcome of a non-binding exchange of information.

**Cooperation**: Cooperation is modeled by global optimization with full information about credit benefits and conservation costs. The details of the optimization procedure are described in Appendix A.

Step by step, the decisions of all agents are collected and the resulting ecological value $U$ as given in Eq. (5) is compared with the demand $D$ (Eq. (7)). The emergence of an equilibrium between demand and supply is modeled by repeatedly adjusting the market price $P$ in Eq. (11) until demand and supply are balanced. The order in which agents are asked is randomized at every timestep, but does not change while the market price is adjusted. Fig. 2 shows a flow diagram of the processes within one timestep.

Simulation runs were initialized with a random landscape configuration which delivered the target supply of conservation. A series of tests showed that the initial configuration has no influence on the resulting landscape after several hundred time steps. This holds true also for non-random start configurations. Data acquisition was started after 600 trading steps to ensure that the simulation had reached its steady state. The results show the mean of 50 runs. Standard deviations for all values were calculated but omitted in the figures because they were very small.

## 4. Analytical approximations—clusters and disorder

Although the number of landscape configurations which fulfill the conservation target is extremely large, two structures are

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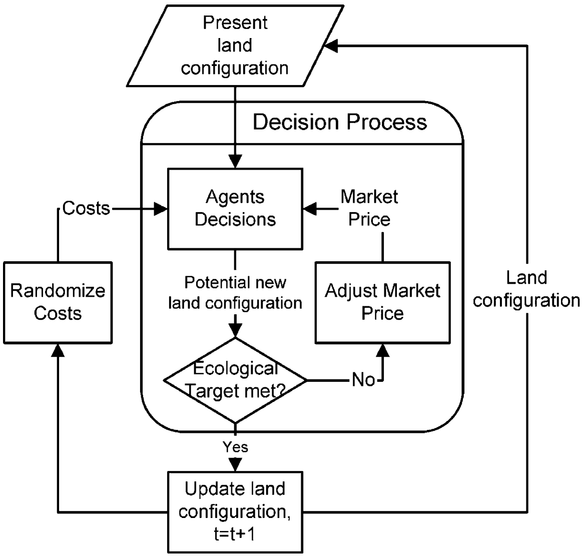

**Fig. 2.** Flow diagram of processes within one timestep.

particularly simple and their properties may be calculated analytically: one is a landscape where habitats are concentrated into one big cluster, the other is a landscape where habitats are scattered according to the lowest costs. Examples of these states will appear later in the results (Fig. 3). Clustering and disorder mark the extreme cases of possible connectivity values: No other state produces more connectivity than a cluster, and no reasonable state (leaving aside anticorrelated structures) produces less connectivity than the scattered, disordered state. It will prove useful for the interpretation of the results to derive some analytical approximations for these two states.

### 4.1. Critical $\delta$ value for clustering

Let us assume that agents can only choose between clustering and spread. Clustered structures lead to a higher credit value per cell, but also to higher average costs, because a spread, disordered configuration can more effectively allocate conservation efforts on the sites with the lowest costs. At low values of cost heterogeneity $\delta$ compared to connectivity weight $m$, a clustered structure is clearly favored. At increasing cost heterogeneity, we expect a critical value $\delta^c$ where the net benefits from clustering become smaller than the net benefits from spread.

We can derive this critical value by equating the worst benefit-cost ratio of cells within a cluster with the best ratio of an isolated cell. In a cluster, the habitats with the highest costs have $c = 1 + \delta$, while outside the cluster, the cells with lowest costs have $c = 1 - \delta$. The ecological value of a clustered and a disordered cell is given by Eqs. (3) and (2). Hence, we obtain

$$\frac{1}{1+\delta^c_{add}} = \frac{1-m}{1-\delta^c_{add}} \Rightarrow \delta^c_{add} = \frac{m}{(2-m)}, \tag{12}$$

$$\frac{1+m}{1+\delta^c_{mar}} = \frac{1-m}{1-\delta^c_{mar}} \Rightarrow \delta^c_{mar} = m \tag{13}$$

as critical values for additive and marginal incentives, respectively.

### 4.2. Clustered and disordered cost level

Further, we are also interested in the costs of maintaining the land at either of the two states. Cells in a cluster have 8 neighbors and therefore yield an average ecological value of $(1-m) + m\beta = 1$ per cell (Eq. (5)). Therefore, a number of $\lambda N$ patches satisfies the fixed demand of $\lambda$ per cell (Eq. (7)). As costs are spatially uncorrelated, the mean costs $\bar{c}_p$ within a cluster are approximately equal to the mean costs of the landscape (for the chosen function $\bar{c}_p = 1$) as long as finite size effects can be neglected. Thus, the total costs of satisfying the demand of $\lambda N$ credits through a cluster are

$$C_{clu} = \frac{1}{N} N\lambda = \lambda. \tag{14}$$

This means that the costs for a cluster are simply constant and proportional to its size. In a disordered state of density $\alpha$, occupied sites are distributed randomly according to the lowest costs. Each occupied cell has on average $8\alpha$ neighbors, leading to an average credit value of $(1-m) + m\alpha$ per grid cell. To reach an average credit supply of $\lambda$ per cell, we require that

$$\alpha[(1-m) + m\alpha] = \lambda. \tag{15}$$

Solving for $\alpha$ yields

$$\alpha = \frac{-1+m+\sqrt{(-1+m)^2+4m\lambda}}{2m}. \tag{16}$$

When the cells with the lowest costs are selected first, the marginal costs $c_p(\zeta)$ increase with the fraction $\zeta$ of cells which are selected. With costs being uniformly distributed across the interval $[1-\delta \ldots 1+\delta]$, $c_p(\zeta)$ is given by

$$c_p(\zeta) = (1-\delta) + 2\delta\zeta. \tag{17}$$

From this, we can derive the total costs for a disordered state as

$$C_{do} = \alpha \int_0^{\alpha} c_p(\zeta)\, d\zeta = \alpha - (\alpha - \alpha^2)\delta. \tag{18}$$

Thus, the costs for a disordered state are dependent on the cost heterogeneity $\delta$ and are linearly decreasing with $\delta$. The cost lines for the clustered and the disordered state mark an upper boundary for cost-effective configurations in Figs. 5 and 6. As a function of $\delta$, they intersect at

$$\delta = \frac{\alpha - \lambda}{\alpha - \alpha^2} = m, \tag{19}$$

where the second equality is derived from inserting the expression in Eq. (16) for $\alpha$. Note that the final result, $\delta = m$, coincides with the critical point for marginal incentives (Eq. (13)).

## 5. Simulation results

### 5.1. Critical values

When analyzing the parameter space of $m$ and $\delta$, we observe steep transitions of all aggregated state variables along a curve of critical value pairs $(\delta^c, m^c)$. Parameter values beyond this curve lead to disordered landscape structures, while values below $\delta^c$ lead to ordered, connected structures. The shape of the transition curve in the space of $m$ and $\delta$ differs for additive and marginal incentives. Fig. 3 shows the simulation results for additive and marginal incentives at $\lambda = 0.1$ together with the analytically derived curves Eqs. (12) and (13). The right side of Fig. 3 shows a vertical cross-section of the left hand side plots in $\delta$-direction at $m = 0.5$. The transition values $\delta^c$ in this curve agree with the analytical approximations from Eqs. (12) and (13) (Table 3).

The introduction of coordination (submodel b.1 and b.2) leaves these results largely unchanged. Fig. 4 shows that coordination only slightly decreases the steepness of the transition, but does not

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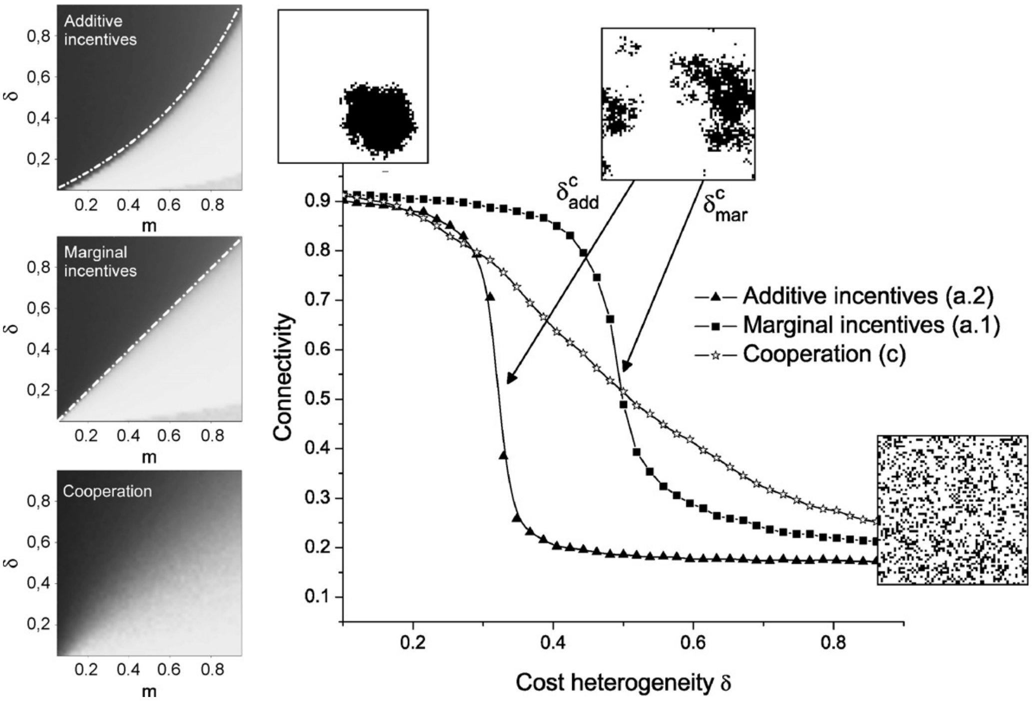

**Fig. 3.** On the left, landscape connectivity $K$ (Eq. (9)) for marginal incentives (top), additive incentives (middle) and cooperation (bottom) as a function of cost heterogeneity $\delta$ and connectivity weight $m$ at $\lambda = 0.1$. Darker colors indicate lower connectivity. Dotted lines display the theoretical curves as given in Eqs. (12) and (13). The right graph shows a cross-section of the three plots in $\delta$ direction at $m = 0.5$ together with typical landscape structures emerging from the simulations in the three domains: Clusters (left), transition states (middle) and disorder (right). The two arrows indicate that the transition state appears at different levels of $\delta$, depending on the chosen incentive mechanism.

change the transition point. In contrast to that, cooperative decisions lead to a rather broad, nearly linear transition for the same parameter values.

### 5.2. Cost-effectiveness

A second question was how the three behavior options would perform in terms of costs needed to reach an equal amount of conservation credits. Fig. 5 shows the total conservation costs as a function of cost heterogeneity $\delta$ at $m = 0.5$, together with the theoretical cost levels for the clustered and the disordered states as calculated in Eqs. (14) and (18) (dotted lines). Noticeably, the cost function of additive incentives displays a hump around the transition area (Fig. 5), leading to approximately 20% higher costs for additive compared to marginal incentives. Considering the theoretical cost functions for the ordered and the disordered states (Eqs. (14) and (18)), the reason becomes evident: under marginal incentives, agents switch from clustering to disorder right at the point where the costs of a cluster and the costs of a disordered state intersect (Eq. (19)). In contrast, under additive incentives, agents switch to disordered configurations earlier at a lower level of cost heterogeneity $\delta$. At this point, the cost level of a disordered configuration is still considerably higher than that of a clustered one, resulting in efficiency losses in this area.

**Table 3**
Critical value $\delta^c$ (measured as $\delta$ at half transition) at $m = 0.5$ from Fig. 3 together with theoretical expectations.

| Model | Simulation | Approximation |
|---|---|---|
| Additive incentives | 0.33 ± 0.02 | 0.33 |
| Marginal incentives | 0.50 ± 0.02 | 0.5 |

### 5.3. Influence of behavior on costs

The inefficiency which has been observed for additive incentives is to a great extent mitigated by the introduction of coordination (Fig. 6). For a value of 10 communication steps per trading period, only small differences between additive and marginal incentives remain. This stems mainly from a better adaptation of land use to the current costs. Transition points and

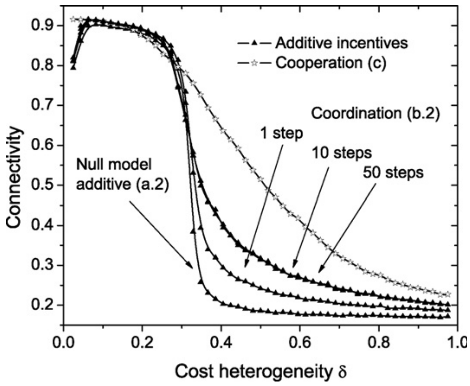

**Fig. 4.** Connectivity $K$ (Eq. (9)) as a function of cost heterogeneity $\delta$ at a fixed $m = 0.5$. It can be seen that increased communication does not affect the critical point $\delta^c$ of the additive incentive curves.

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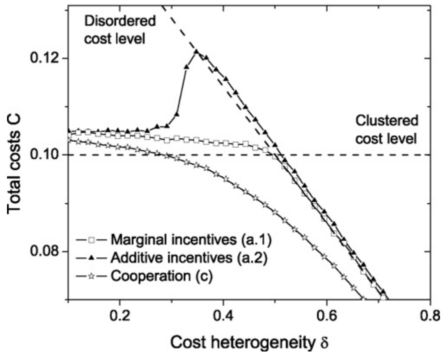

**Fig. 5.** Total conservation costs as a function of cost heterogeneity $\delta$ at $m = 0.5$ and $\lambda = 0.1$ (solid lines) together with theoretical costs for the clustered and the disordered state (dashed lines).

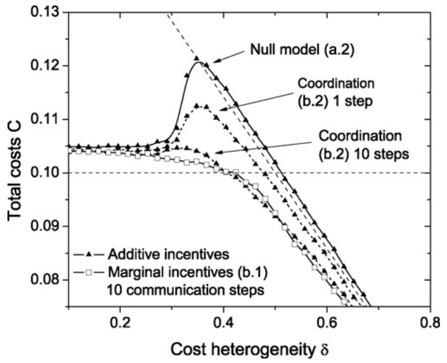

**Fig. 6.** Effect of coordination: plottet are the total conservation costs as a function of cost heterogeneity $\delta$ at $m = 0.5$ and $\lambda = 0.1$. With increasing coordination steps, the costs of additive incentives approach the costs of marginal incentives.

thus the landscape structure remain largely unchanged by coordination as shown in Fig. 4.

The total conservation costs under cooperation are considerably lower than for the other options (Fig. 5). They differ mostly around the critical values $\delta_c$, where optimal decisions are more difficult to obtain than for extreme values of $\delta$ where one allocation pattern (cluster or disorder) is clearly favored.

## 6. Discussion

### 6.1. Main findings

The aim of this modeling study was to examine the effect of simple spatial incentives and social organization on the emerging landscape structures and on the total cost of a conservation market. We introduced an agent-based model of a conservation market with spatial incentives. The model enabled us to compare different spatial incentives (additive and marginal) and different types of agent behavior, including individual and collective decision processes. By individual decisions, we mean that agents decide individually according to their costs and benefits, while collective decisions consider the costs and benefits of the whole group.

Our results show that rewarding more conservation credits when other conservation sites were directly connected to the focal site could effectively influence the larger scale structure of conservation measures. The connectivity weight $m$, which determines the amount of credits which are rewarded for conservation, acts as a control parameter that determines the clustering of habitats in the landscape. The exact shape of this response depends on the heterogeneity of conservation costs, the incentive mechanism, and the assumed behavior of agents (Fig. 3).

Individual decision processes with low information (null model a.1 and a.2) lead to a partitioning of the parameter space, each producing very distinct landscape patterns, separated by a small transition area. These predominant patterns are a completely clustered state, appearing when cost heterogeneity $\delta$ is low compared to the connectivity weight $m$, and a completely disordered state, emerging when $\delta$ is high compared to $m$. The reason for the stability of these two states in a dynamical and heterogeneous cost background lies in the fact that, starting from one of them, agents repeatedly end up in a very similar configuration, since trading stops as soon as a local cost optimum is found. Decision processes with more information (coordination b.1 and b.2) explore a wider range of options, but even in the case of coordination with a large number of communication steps, agents stop trading once trade cannot improve the position of any single agent (Fig. 4). Only cooperating agents (submodel c) completely avoid getting stuck in local suboptima and produce a more linear response to the control parameter $m$ (Fig. 3).

The total costs expected to reach the same amount of conservation credits are significantly different between marginal and additive incentives in markets with low information, particularly in the transition regime (Fig. 5). This strong cost increase originates from the too early abandonment of clusters under additive incentives. At increased levels of coordination, the cost differences between additive and marginal incentives are considerably reduced (Fig. 6). The most efficient allocation of conserved sites is achieved through collective decisions (cooperation), where the configuration space is explored in a way which avoids getting stuck in local minima (Fig. 5) and differences between marginal and additive incentives disappear.

### 6.2. Assumptions and generality of the results

A prerequisite for the difference between marginal and additive incentives is that the ecosystem changes created by the market are not marginal. If changes were marginal, such that all interactions between sites are approximately unchanged by the actions induced by the market, one may simply use the marginal value as a basis for the evaluation, also in the case of fixed price payments schemes. For most real-world situations, however, it is likely that actions induced by the market interact. In such cases, it may be beneficial to implement incentives that explicitly include interactions between sites.

For such cases, we view the model presented in this paper as a generic model for the supply side of a spatial conservation market. The reader may have noted that we have fixed the supply, i.e. the amount of credits produced at each time step (Eq. (7)). One might suggest that the model should therefore be rather interpreted as the special case of a tradable permit market or an auction, where the amount of credits is fixed and prices vary. However, we could equally have fixed the costs of conservation, as was done with the same model in (Hartig and Drechsler, 2009). Within the model assumptions, both options (fixing prices or quantities) are equivalent, because fixed prices result in a fixed amount of credits and vice versa. We therefore think that the model is generic for the way spatial incentives act on the spatial allocation of conservation measures and does not make any assumptions which would require that it be interpreted as a

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specific market form such as an auction, a payment scheme, or a permit market.

One assumption made in the model is that conservation costs are uncorrelated in time, as implied by the random sampling of costs from the uniform distribution at each step of the simulation process. While strong yearly changes of costs may occur in some situations, e.g. when farmers are using land that needs to rest for conservation, totally uncorrelated costs are, in general, rather unlikely. The results, however, qualitatively prevail in the case of cost correlations. Although not presented, we applied an unsystematic analysis of temporal and spatio-temporal correlation of costs as they were used in (Hartig and Drechsler, 2009). Temporal correlation of costs acts similarly to increasing coordination steps in our model. This can be understood when considering that increasing coordination is essentially a temporal correlation of costs, as costs are fixed during the time of communication. Additional spatial cost correlation further decreases the efficiency losses associated with individual decisions. We assume that the reason for this is the spatial smoothing of the costs. When the cost correlation length is large compared to the correlation of the incentives, the chances of getting stuck in a local minimum decrease rapidly.

There are a number of abstractions from reality regarding the behavior of agents. First of all, for all three behavior models, we assumed that there are no additional costs associated with decisions and information exchange. Secondly, we assumed that agents are fair. In reality, both coordination through cheap talk and cooperation present possibilities to strategically exploit other agents. Cheap talk includes the possibility of strategic lies. Agents may try to induce their neighbors to make the first move towards conservation so that they themselves can subsequently free-ride. Cooperation requires landowners to reveal their true costs and temporarily accept lower payoffs if, in exchange, the group payoff is increased. Payments between landowners (side payments) could compensate for these losses, but the question of how this kind of cooperative system should be organized and whether it is stable against exploitation by defectors and free-riders remains open. One could, however, hope that stabilizing mechanisms such as reputation (Fehr and Schmidt, 1999; Sigmund et al., 2001; Milinski et al., 2002) may improve cooperation at least when defection is observable for neighbors. However, if defection is only detectable indirectly, support for persistent cooperation would be much weaker. Experimental studies as proposed in Hartig et al. (in press) could help to study which of these strategies are most likely to be realized by human agents.

Finally, very important for real-world conservation are restoration costs and time lags for restoration. In this model, we assumed that land use can be changed instantaneously and without costs. The inclusion of costs and the time lags associated with habitat restoration appears to be an interesting problem for future research.

### 6.3. Policy implications

Market-based instruments are increasingly applied for biodiversity conservation on private lands. At present, conservation markets seldom include spatial interactions between sites. One reason for this is that the inclusion of interactions increases transaction costs, i.e. costs associated with organizing the trading (Salzman, 2005; Jack et al., 2008). On the other hand, even simple spatial incentives may provide considerable efficiency gains for maintaining biodiversity by means of market-based instruments (Hartig and Drechsler, 2009). Our results suggest that it is possible to control larger scale landscape structures with relatively simple spatial incentives. We tested two different spatial incentive mechanisms. Marginal incentives are dependent on the order of trading and therefore rather qualify for markets where trading takes place sequentially and the contract length is long, such as, for example, in tradable permit markets. Additive incentives are slightly simpler and qualify better for schemes where transactions are performed in parallel and the contract length is short, such as yearly payments. In the case of perfectly cooperating landowners, both options yield the same result. If landowners decide individually, however, marginal incentives generally perform better than additive incentives.

Therefore, the two main messages for policy are: (1) The reaction of landowners to spatial incentives is likely to differ with social organization and the applied incentive mechanism. (2) Besides changing the incentives, a market design that encourages cooperation seems beneficial when applying spatial metrics in market-based instruments.

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## Appendix A. Optimization

To model a perfectly rational cooperating group of agents, we performed a global optimization of the land configuration. We used a slightly modified simulated annealing algorithm, which delivered better results than the original algorithm by Kirkpatrick et al. (1983). The goal of the optimization was to minimize the total conservation costs as defined in Eq. (10) under the constraint of satisfying the fixed demand as given in Eq. (7):

$$\min\left\{\sum_{i=1}^{n}\sigma_i c_i(t)\right\}_{U=\lambda N}. \tag{20}$$

A random site $x_i$ was occupied with probability

$$p(\sigma_i, T) = \min\left(1, e^{-\phi_i(\sigma_i)-\Phi/T}\right), \tag{21}$$

where $\phi_i(\sigma_i)$ is the marginal benefit-cost ratio of site $x_i$ and $\Phi$ is the average benefit-cost ratio of the present configuration. The simulated annealing was performed in $n$ steps with a new random subset of $N\nu$ of the sites at each step. To satisfy the constraints, each step was followed by adding (removing) conserved sites starting with the sites of highest (lowest) $\phi$ until the target value of $U = \lambda N$ was met. Temperature decay was exponential with decay parameter $\tau$ per time step. Table A.1 lists the parameter values used.

**Table A.1**
Optimization parameters chosen for the simulated annealing.

| Parameter | Connotation | Value |
|---|---|---|
| $T_0$ | Start temperature | 3 |
| $\tau$ | Decay parameter | 0.001 |
| $n$ | Steps | 3500 |
| $\nu$ | Fraction of sites | 0.5 |

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## References

Acharyya, M., 1998. Nonequilibrium phase transition in the kinetic Ising model: dynamical symmetry breaking by randomly varying magnetic field. Phys. Rev. 58 (1), 174–178 doi:10.1103/PhysRevE.58.174.

Ando, A., Camm, J., Polasky, S., Solow, A., 1998. Species distributions, land values, and efficient conservation. Science 279 (5359), 2126–2128 doi:10.1126/science.279.5359.2126.

Chomitz, K.M., 2004. Transferable development rights and forest protection: an exploratory analysis. Int. Regional Sci. Rev. 27 (3), 348–373 doi:10.1177/0160017604266030.

Drechsler, M., 2009. Predicting metapopulation lifetime from macroscopic network properties. Math. Biosci. 218 (1), 59–71 doi:10.1016/j.mbs.2008.12.004.

Drechsler, M., Wätzold, F., 2009. Applying tradable permits to biodiversity conservation: effects of space-dependent conservation benefits and cost heterogeneity on habitat allocation. Ecol. Econ. 68 (4), 1083–1092 doi:10.1016/j.ecolecon.2008.07.019.

Drechsler, M., Wätzold, F., Johst, K., Bergmann, H., Settele, J., 2007. A model-based approach for designing cost-effective compensation payments for conservation of endangered species in real landscapes. Biol. Conserv. 140 (1–2), 174–186 doi:10.1016/j.biocon.2007.08.013.

Engel, S., Pagiola, S., Wunder, S., 2008. Designing payments for environmental services in theory and practice: an overview of the issues. Ecol. Econ. 65 (4), 663–674 doi:10.1016/j.ecolecon.2008.03.011.

Faith, D.P., Carter, G., Cassis, G., Ferrier, S., Wilkie, L., 2003. Complementarity, biodiversity viability analysis, and policy-based algorithms for conservation. Environ Sci. Policy 6 (3), 311–328 doi:10.1016/S1462–9011(03)00044–3.

Faith, D.P., Walker, P.A., 1996. Integrating conservation and development: effective trade-offs between biodiversity and cost in the selection of protected areas. Biodivers. Conserv. 5 (4), 431–446 doi:10.1007/BF00056389.

Farrell, J., Rabin, M., 1996. Cheap talk. J. Econ. Perspect. 10 (3), 103–118.

Fehr, E., Schmidt, K.M., 1999. A theory of fairness, competition, and cooperation. Q. J. Econ. 114 (3), 817–868.

Frank, K., Wissel, C., 2002. A formula for the mean lifetime of metapopulations in heterogeneous landscapes. Am. Nat. 159 (5), 530–552.

Galam, S., Zucker, J.D., 2000. From individual choice to group decision-making. Physica A 287 (3–4), 644–659 doi:10.1016/S0378–4371(00)00399-X.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jorgensen, C., Mooij, W.M., Muller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Ruger, N., Strand, E., Souissi, S., Stillman, R.A., Vabo, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. Ecol. Model. 198 (1–2), 115–126 doi:10.1016/j.ecolmodel.2006.04.023.

Hartig, F., Drechsler, M., 2009. Smart spatial incentives for market-based conservation. Biol. Conserv. 142 (4), 779–788 doi:10.1016/j.biocon.2008.12.014.

Hartig, F., Horn, M., Drechsler, M., in press. EcoTRADE—a multi player network game of a tradable permit market for biodiversity credits. Environmental Modelling and Software. doi:10.1016/j.envsoft.2009.01.003.

Hausmann, J., Rujan, P., 1997. Stationary properties of a randomly driven Ising ferromagnet. Phys. Rev. Lett. 79 (18), 3339–3342 doi:10.1103/PhysRevLett.79.3339.

Holyst, J.A., Kacperski, K., Schweitzer, F., 2000. Phase transitions in social impact models of opinion formation. Physica A 285 (1–2), 199–210 doi:10.1016/S0378–4371(00)00282-X.

Imry, Y., Ma, S.-k., 1975. Random-field instability of the ordered state of continuous symmetry. Phys. Rev. Lett. 35 (21), 1399–1401 doi:10.1103/PhysRevLett.35.1399.

Jack, B.K., Kousky, C., Sims, K.R.E., 2008. Designing payments for ecosystem services: lessons from previous experience with incentive-based mechanisms. Proc. Natl. Acad. Sci. U. S. A. 105 (28), 9465–9470 doi:10.1073/pnas.0705503104.

Kirkpatrick, S., Gelatt, C.D., Vecchi, M.P., 1983. Optimization by simulated annealing. Science 220 (4598), 671–680 doi:10.1126/science.220.4598.671.

Latacz-Lohmann, U., Van der Hamsvoort, C.P.C.M., 1998. Auctions as a means of creating a market for public goods from agriculture. J. Agric. Econ. 49 (3), 334–345.

MA, 2005. Millenium Ecosystem Assesment: Ecosystems and Human Well-being: Biodiversity Synthesis. Tech. Rep., World Resources Institute, Washington, DC.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405 (6783), 243–253 doi:10.1038/35012251.

Milinski, M., Semmann, D., Krambeck, H.J., 2002. Reputation helps solve the 'tragedy of the commons'. Nature 415 (6870), 424–426 doi:10.1038/415424a.

Mills, D.E., 1980. Transferable development rights markets. J. Urban Econ. 7 (1), 63–74 doi:10.1016/0094–1190(80)90026–1.

Moilanen, A., 2005. Reserve selection using nonlinear species distribution models. Am. Nat. 165 (6), 695–706 doi:10.1086/430011.

Panayotou, T., 1994. Conservation of biodiversity and economic development: the concept of transferable development rights. Environ. Resour. Econ. 4 (1), 91–110 doi:10.1007/BF00691934.

Parkhurst, G.M., Shogren, J.F., Bastian, C., Kivi, P., Donner, J., Smith, R.B.W., 2002. Agglomeration bonus: an incentive mechanism to reunite fragmented habitat for biodiversity conservation. Ecol. Econ. 41 (2), 305–328 doi:10.1016/S0921–8009(02)00036–8.

Salzman, J., 2005. Creating markets for ecosystem services: notes from the field. N. Y. Univ. Law Rev. 80 (3), 870–961.

Salzman, J., Ruhl, J.B., 2000. Currencies and the commodification of environmental law. Stanford Law Rev. 53 (3), 607–694.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. Conserv. Biol. 5 (1), 18–32 doi:10.1111/j.1523–1739.1991.tb00384.x.

Schweitzer, F., Zimmermann, J., Muhlenbein, H., 2002. Coordination of decisions in a spatial agent model. Physica A 303 (1–2), 189–216 doi:10.1016/S0378–4371(01)00486–1.

Sigmund, K., Hauert, C., Nowak, M.A., 2001. Reward and punishment. Proc. Natl. Acad. Sci. USA 98 (19), 10757–10762 doi:10.1073/pnas.161155698.

Sznajd-Weron, K., Sznajd, J., 2000. Opinion evolution in closed community. Int. J. Mod. Phys. C 11 (6), 1157–1165.

Vuilleumier, S., Possingham, H.P., 2006. Does colonization asymmetry matter in metapopulations? Proc. Roy. Soc. B: Biol. Sci. 273 (1594), 1637–1642 doi:10.1098/rspb.2006.3469.

Wunder, S., 2007. The efficiency of payments for environmental services in tropical conservation. Conserv. Biol. 21 (1), 48–58 doi:10.1111/j.1523–1739.2006.00559.x.

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paper V

Florian Hartig, Silvia Wissel, Astrid van Teeffelen, Maarten Hilferink, Martin Drechsler

# Designing market-based incentives to control the fragmentation and dynamics of conservation measures in a real landscape

**in preparation**

**Summary:** We show that spatial incentives and a tax on turnover may effectively control the spatial and the temporal structure of conservation measures in a real landscape under dynamically changing economic conditions.

# Designing market-based incentives to control the fragmentation and dynamics of conservation measures in a real landscape

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**Abstract**

Market-based instruments are environmental policies that are increasingly used to create financial incentives for maintaining natural habitats on private lands. A problem of simple area-based incentives is that there is no direct control of the emerging spatio-temporal allocation of habitats. This raises concerns because the value that is posed by natural habitats can be strongly affected by their configuration in space and time. Therefore, it is an important question how incentives systems may be designed to account for the spatio-temporal allocation of conservation measures. In this study, we simulate a conservation market for wet grasslands and reed marshlands in the Randstad region of the Netherlands. The market includes spatial and temporal incentives that may be adjusted to improve spatial and temporal connectivity of conservation measures, respectively. We find that important ecological landscape characteristics such as the amount of natural habitats, the level of habitat fragmentation and habitat dynamics can effectively be controlled with these incentives. We conclude that explicit spatial and temporal incentives are a policy option to influence emerging landscape characteristics in real world market schemes.

*Key words:* market-based instruments, biodiversity conservation, ecological economic modelling, tradable permits, payments, spatial incentives

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## 1. Introduction

Market-based instruments, also called incentive-based mechanisms (Jack et al., 2008), are environmental policies that create financial incentives for voluntary provision of biodiversity conservation on private lands. For implementing a conservation market, two steps are essential: Defining the traded good and creating demand for this good.

The first step, defining the traded good, refers to the necessity of defining a measure of conservational value. Usually, this is done by providing a function that transforms a set of indicators, e.g. the quality and size of a site, into a value which measures the quantity of conservation provided by a site. Depending on the context, different names are used for the units of this function, such as credits, permits, points or ecopoints. In this paper, we call the conservation units "credits", and we call the function that measures conservation credits the "metric" (Hartig and Drechsler, in press). Measuring the credits provided by different habitats allows us to treat heterogeneous habitats as a commodity that is only differentiated by a single quantity, the credits. Through the credits, habitats are comparable and therefore can be traded on a market. This mechanism is often referred to as commodification or commoditization (Salzman and Ruhl, 2000; Salzman, 2005).

The second step, creating demand for credits, can be achieved by different mechanisms. Broadly, they fall into two classes: Price-based and quantity-based mechanisms (Weitzman, 1974). Price-based mechanisms such as payments (Wunder, 2007; Drechsler et al., 2007; Engel et al., 2008) offer a fixed price for conservation measures. Fixing the price of conservation implies that, unless the regulating authority is omniscient, the quantity of credits produced at the chosen price is uncertain. Quantity-based mechanisms such as auctions (Latacz-Lohmann and Van der Hamsvoort, 1998) or biodiversity offset schemes (Panayotou, 1994; Chomitz, 2004) fix the quantity of credits that are produced by the scheme, but the drawback is that now the price that is necessary to reach this quantity is uncertain.

The main advantage of market-based instruments over top-down approaches such as regulations or planning is that the allocation of conservation measures is not fixed, but may be adjusted by landowners according to their opportunity costs. Assuming that landowners act rational and

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the market for conservation credits is competitive, trading will eventually select those landowners who can provide conservation at the least costs. This promises major cost savings compared to planning approaches.

A problem, however, arises from the fact that the value of conservation measures for species depends on the spatial and temporal allocation of these measures on a larger scale. Therefore, conservation sites cannot be simply compared by their size. Sites are heterogeneous with respect to three main categories: the local value (habitat type and local quality), the spatial context, and temporal context (Salzman, 2005; Wissel and Wätzold, 2008). Ecological research of the last decades has shown that these factors are crucial for the survival of populations. One of the reasons is that most species have limited dispersal abilities and therefore need sufficient spatial habitat connectivity (compare e.g. Saunders et al., 1991; Fahrig, 2002). Moreover, populations rely on temporal continuity of habitat provision (temporal connectivity), because continuous destructions of habitats induce disturbances on populations, even if a similar site is created elsewhere (Hanski, 1999).

One option to account for spatial and temporal processes is setting constraints on local, spatial, and temporal landscape chararacteristics, e.g. by restricting land use change or by awarding credits only for sites with a connectivity above a threshold value. This, however, is unnecessarily restrictive. For ecosystems, there are seldom independent thresholds in certain characteristics, but rather trade-offs between different aspects of the ecosystem. As an example, negative effects of landscape dynamics may be compensated by improving connectivity, or lower connectivity can be compensated by improving the local quality of habitats (Drechsler, 2009).

Although some existing market schemes implicitly include spatial and temporal requirements of species, most incentive-based policies worldwide do not explicitly account for these trade-offs in their incentive mechanisms. But as shown in Hartig and Drechsler (2009), the inclusion of these processes may lead to major efficiency gains. Therefore, it seems promising to examine possible cost saving effects from spatial and temporal incentives in market-based conservation.

A number of previous modelling studies has looked at the effect of including spatial trade-offs (Drechsler and Wätzold, 2009; Hartig and Drechsler, 2009) and temporal trade-offs (Drechsler and Hartig, submitted) in market-based instruments. A limitation of these studies was that they worked on artificially created cost data. The reason for this is that reliable empirical data regarding the distribution and the dynamics of opportunity costs for conservation is very difficult to gather (Polasky, 2008), specially on the spatial resolution of single landowners. Another simplification of existing studies is that costs are assumed to be external, meaning that there are no feedbacks between conservation costs and the environmental policy. Yet, as Polasky (2006) notes, policy instruments may create feedbacks on land prices, e.g. when an increasing scarcity of land, created by a conservation policy, leads to an increase of the overall price level.

The aim of this study is to find out whether spatial and temporal incentives can effectively control the spatial structure and the dynamics of voluntary conservation measures in a real landscape, and how such a conservation market influences economic conditions. To answer these questions, we extend an existing model that simulates land use choices in the Netherlands between 2003 and 2040. The simulation approach is novel in three respects: It is one of the first studies that simulates the effects of spatial conservation incentives on a large realistic landscape, it contains dynamic changes of land prices in the future, and it contains feedback effects of the conservation measures on land prices. We find that spatial and temporal incentives may effectively control fragmentation as well as the amount of reallocation of habitats in the landscape.

## 2. Methods

### *2.1. Overview*

The Green Heart is a ca. $1900 km^2$ large, mainly agriculturally used area in the Randstad region of the Netherlands. It is surrounded by the cities of Amsterdam, The Hague, Rotterdam and Utrecht (Fig. 1). In contrast to the highly urbanized surroundings, the Green Heart is relatively open and hosts mainly intensive dairy farming, but is also home to biotopes such as wet grasslands, peat lands, reed marshes, and open water. As such, it is an important area for rare species that depend on the according habitat types. Increasing urbanization and agricultural intensification put large pressure on the Green Heart, and the preservation of the rare habitats and species in the area is a major concern. More details on the study area can be found in Appendix A.1.

The aim of this modelling study is to simulate the effects of a spatially and temporally targeted market-based conservation policy in the Green Heart. By spatially and temporally targeted, we mean that the market sets incentives not only for the amount of area that is used for conservation, but also for the spatial allocation of these habitats with respect to each other, and the amount of habitat reallocations. The model is implemented in the GeoDMS software, an open framework for GIS modelling. We used an existing economic model implemented in the GeoDMS as a base for simulating land use choices. Building on this, we include additional land use options that create conservation credits and implement a market with a price mechanism that aims at fulfilling a fixed demand for conservation

**Figure 1:** Study area: The border of the Green Heart is marked by a dark line. Surrounding, we see the cities of Amsterdam, The Hague, Rotterdam, and Utrecht.

credits. Changes of land use during the simulation time are induced by changes of the economic boundary conditions during the simulation period from 2003 to 2040. More details on the model and the software can be found in Appendix B.

The following subsections give an overview of the state variables of the model (2.2), the economic land use model (2.3), the implementation of the conservation market (2.4) and the methods applied for analyzing the simulation runs (2.5).

### *2.2. State variables and scales*

The model is grid-based and simulates the land use in the whole Netherlands with a resolution of $100m \times 100m$ ($3250 \times 2700$ grid cells, $325km \times 270km$). For each grid cell, there are 30 land use options (Table 2). At each time step, the state of the simulation is given by the information which of the 30 possible land use types are currently allocated to each grid cell. 28 of the land use types are derived from (MNP, 2007). Additionally, we included the option to create conservation measures for reed marsh and wet grassland. In the following, we label the land use type with the index $k$.

Land use change and reactions to conservation incentives are simulated from 2003 to 2040. The reason for starting in the year 2003 was data availability. Within the next 37 years, external economic conditions and infrastructure change based scenarios of a scenario of economic development. Details are described in the next subsection and in Appendix B.3. The simulation time steps are 0.5 years.

### *2.3. Economic land use model*

Within the economic model, the central quantity that decides on the allocation of land use is called the socio-economic suitability $Y_i^k(t)$. The socio-economic suitability $Y_i^k(t)$ of land use type $k$ for grid cell $i$ at time $t$, calculated in $€/m^2/yr$, derives from three quantities: hedonic suitabilities $H_i^k(t)$, conversion costs $C_i^k(t-1)$ and shadow prices $p_i^k(t)$.

$$Y_i^k(t) = H_i^k(t) + C_i^k(t-1) + p_i^k(t) \tag{1}$$

Hedonic suitabilities $H_i^k(t)$ represent a hedonic (scarcity independent) use value of cell $i$ for land use type $k$. Hedonic utilities are calculated from the spatial information that is present in the model, e.g. current land use in the vicinity, soil conditions or distance to infrastructure. Also, they may encompass possible management costs for the respective land use type. $C_i^k(t-1)$ represents conversion costs that depend on the former land use of the focal grid cell at timestep $(t-1)$. Hedonic suitabilities and conversion costs make up what we call the net economic benefit $B_i^k(t)$:

$$B_i^k(t) \equiv H_i^k(t) + C_i^k(t-1)\ . \tag{2}$$

The second part of the socio-economic suitability is a positive or negative shadow price $p^k(t)$. In economics, a shadow price is a price that originates from certain constraints which are put on an optimization. In this model, the shadow prices originate from the possibility to set minimum and maximum constraints $\Gamma^k(t)$ for $S^k$, the total amount of allocated land of each land use type $k$. Minimum constraints act like a completely inelastic demand for a certain land use, which creates a positive shadow price $p^k(t)$ if the allocated land use of $k$ drops under a minimum $\Gamma_{min}^k(t)$. Maximum constraints create a negative shadow price $p^k(t)$ if the allocated amount $S^k$ exceeds $\Gamma_{max}^k(t)$. The constraints $\Gamma^k(t)$ may originate from the demand on the market itself, for example because housing is essential for market participants and the willingness to pay therefore increases if housing gets scarce. The constraints may, however, also represent societal preferences and governmental policies. Reasons for this could for example be a desire for having a limit on land use that is detrimental for the environment, or a minimum of land use that is important for recreation or landscape beauty. Therefore, $Y_i^k(t)$, although measured in $€/m^2/yr$, should not be interpreted as a market price of land. Rather, it is a measure of suitability of land use given economic benefits, expressed by $H_i^k(t)$ and $C_i^k(t-1)$, and some additional constraints, expressed by $p_i^k(t)$, that may include scarcity, but also governmental regulations.

The model then optimizes the land use based on these suitabilities, assuming perfect information of all landowners,

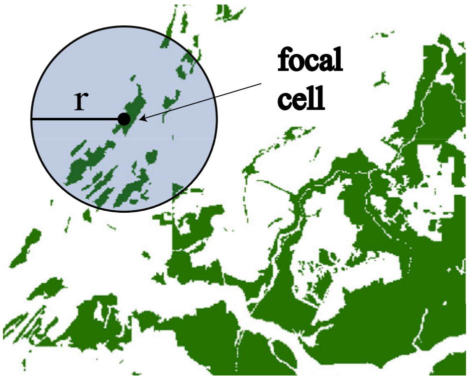

**Figure 2:** Connectivity measure: Connectivity is calculated as the fraction of cells within a circle of radius $r$ around the focal cell that are managed as the same habitat type as the focal cell.

and assuming that the conditions of the current time steps are representative for the future. At each time step, the suitabilities of each land use type are calculated and the land use that yields the highes socio-economic suitability $\hat{Y}_i^k(t)$ is chosen.

$$\hat{Y}_i^k(t) \geq Y_i^j(t) \forall k, j \in k[0, 1, ...29], k \neq j \tag{3}$$

Here, as in the rest of the paper, a hat on top of a variable denotes that this variable refers to the allocated (chosen) landuse type. As an example, there is a possible net benefit $B_i^k(t)$ for each land use type $k$, but the $\hat{B}_i^k(t)$ refers to the net benefit for the land use type $k$, which was allocated by the simulation on this grid cell at time step $t$ according to eq. 3.

To keep the supply within the constraints $\Gamma^k(t)$, the shadow price $p^k$ for each land use type $k$ is adjusted in an iterative process until all constraints are satisfied (Kuhn and Tucker, 1951). MNP (2007) defined three different sets of hedonic utilities $H_i^k(t)$ and constraints $\Gamma^k(t)$ for the years 2010, 2020 and 2040. To create a continuous dynamic scenario, we interpolated the constraints $\Gamma^k(t)$ linearly between these years. The net economic benefits $B_i^k(t)$ was assumed to be constant within each period. The data from MNP (2007) was included such that the $B_i^k(t)$ that were calculated for 2010 are valid between 2003 and 2010, the $B_i^k(t)$ for 2020 are valid between 2010 and 2020, and the $B_i^k(t)$ for 2040 are valid between 2020 and 2040. The dynamical allocation is created by recalculating the market equilibrium under the changing external factors in time steps of 0.5 years. Details can be found in Appendix B.3.

### *2.4. Implementation of the conservation market*

In the model, two conservation land use types are implemented. These are the management for wet grassland and as reed marsh habitats. When managing their land as one of them, landowners receive conservation credits per grid cell that are calculated according to the following formula:

$$s_i^k = \left[(1 - m^k) + m^k \cdot \zeta_i^k(r^k)\right] \cdot \Theta_i^{Zone} \cdot \Theta_i^k \tag{4}$$

The last two factors $\Theta_i^{Zone}$ and $\Theta_i^k$ are 0 if the cell is either not in the study area or not suitable for the habitat type $k$, and 1 otherwise (See appendix A.1 and A.3 for details). The connectivity weight $m^k$ can be used to vary how much connectivity is incorporated into the calculation of the awarded conservation credits for habitat type $k$ (Hartig and Drechsler, 2009; Drechsler and Wätzold, 2009): increasing $m^k$ decreases the value of $(1-m^k)$, which is a base benefit independent of connectivity, in favor of $m \cdot \zeta_i(r^k)$ which is a reward for the connectivity $\zeta_i(r^k)$ of the grid cell. The connectivity $\zeta_i(r^k)$ is measured by the proportion of conserved sites within a circle of radius $l$ (see also Fig. 2):

$$\zeta_i^k(r) \equiv \left( \sum_{d_{ij} < r^k} \sigma_j^k \right) \cdot (A(r^k))^{-1} . \tag{5}$$

where the $\sigma_j^k$ is 1 if the grid cell $i$ is managed as habitat type $k$, $d_{ij}$ is the euclidian distance between grid cell $i$ and $j$, and the factor $A(r) = \sum_j d_{ij} < r^k$ normalizes $\zeta$ with the area of the grid cells within the connectivity radius, so that the maximum value of $\zeta$ is one (Hartig and Drechsler, 2009).

To define a socio-economic suitability for conservation land use, we introduce for each conservation type a market price $p^k$ for conservation credits. The reason why these market prices are labelled like the shadow prices of other land use types will become apparent in the next paragraph. Additionally, we introduce conversion costs, maintenance costs and the possibility to raise a tax on the conversion of habitats. The tax acts per credit, which means that, if a habitat is newly created, the credit price is reduced by the tax. This discourages reallocation of habitats in favor of keeping existing habitats in their location. Combining all factors, the socio-economic suitability of allocating the i-th grid cell to the respective habitat type $k$ is given by

$$Y_i^k(t) = s_i^k \cdot (p^k - T^k(t-1)) - C_i^k(t-1) - M^k \tag{6}$$

Here, $s_i^k$ is the ecological utility from eq. 4, $p^k$ is the market price for habitat type $k$, $C_i^k(t-1)$ and $T^k(t-1)$ are conversion costs and taxes, respectively, that only appear when the cell was not managed as land use type $k$ before, and $M^k$ are management costs (see appendix A.4 for details on the calculations of these costs).

Market prices for conservation are assumed to arise from a fixed, completely inelastic demand $D^k$ for conservation credits, meaning that the demand for conservation credits is always the same, irrespective of the price. Such a completely inelastic demand could originate e.g. from a biodiversity offset scheme, or from a conservation authority that tries to buy the same amount of conservation credits each year (Hartig and Drechsler, in press). $D^k$ acts similar to the constraints $\Gamma^k$, in that it puts an upper and a lower limit on the production of credits (the upper limit arises from the assumption that no landowner would produce more credits than he could sell on the market). However, unlike for the $\Gamma^k$, this constraint does not act on the habitat area, but on the credits that stand for habitat quality (eq. 4). To keep the supply of credits $S^k$ in balance with the fixed demand, we introduce a number of iterations that are used to test the reaction of landowners to the current price and adjust the price if necessary. At each iteration, the deviation between target level and actual credit level is calculated

$$\Delta S^k = S^k - D^k \tag{7}$$

and the market price $p^k$ is adjusted unless the target for the credits is met. The details of the adjustment are discussed in Appendix B.4 and B.4.

### *2.5. Analysis Method*

The influence of the incentives in the model was analyzed by a $3 \times 3 \times 3$ factorial design, i.e. with all possible 27 combinations of connectivity weight at $(0, 0.5, 1)$, connectivity radius $(200, 500, 1000)$ and turnover tax $(0, 3, 7)$. We view the incentive combination of connectivity weight $m^k = 0.5$, connectivity radius $l = 1km$, and conversion tax $T = 3$ as the base combination. Both habitat types (grasslands and marshlands) always received the same spatio-temporal incentive, but they differed in their demand $D^k$. For $m$, $l$ and $T$, where grass and marsh have the same parameters, we omit the index $k$ in the following analysis. For each run, the demand was $D^k$ was determined by calculating the amount of credits for both habitats types at the initial state. Note that this means that $D^k$ changes when the values of the metric are changed.

An important quantity for practical conservation applications are the costs of different conservation options. As mentioned above, the suitabilities $\hat{Y}_i^k(t)$ that are used to determine the allocated land use should not be interpreted as market prices for land, because they depend on the shadow prices $p_i^k(t)$. Rather than costs, $p_i^k(t)$ may be viewed as an indicator of how much intervention in terms of shadow prices we need to keep the land use decisions based on $B_i^k(t)$ within the constraints $\Gamma^k(t)$. One possible measure that acts similar to costs is the loss of economic net benefit $\hat{B}_i^k(t)$ (eq. 2) that is caused by the conservation scheme. $\hat{B}_i^k(t)$ may be viewed as a measure of economic output realized by the current land use. We call the sum of the $\hat{B}_i^k$ of the current allocation over all grid cells $B$:

$$B = \sum_{i,k} \hat{B}_i^k \ . \tag{8}$$

Differences in $B$ between different scenarios suggest a loss of economic output in the region and may be interpreted as societal costs of different policy alternatives.

## 3. Results

### *3.1. Spatial incentives and spatial pattern*

Fig. 3 shows the spatial land use allocation of the base incentive combination, together with more detailed maps of a subregion of the study area, for comparing the base incentive combinations with incentive combinations of lower and higher connectivity weights $m$. The results show that the value of the connectivity weight has a strong influence on the degree of clustering in the landscape. A low $m$ leads to very spread habitat configurations, while a high $m$ leads to very compact, clustered allocations of habitat. For cases with high connectivity weight $m$, the absolute habitat is slightly decreasing during the first time steps, because reallocations of habitats into clusters decreases the area necessary to fulfill the fixed demand $D^k$ for credits (eq. 7).

### *3.2. Temporal incentives and temporal pattern*

There are three main factors that lead to a reallocation of habitats. One is economic change in the region, which occurs during the simulation time. The second factor is immediate the adjustment of land use to the incentives that are created by the market. The third reason is the transition from the initial state of the simulation to the first simulation time step. Even if there are no spatial incentives, we see some reallocation of habitat. The reasons for this are examined in more detail in the discussion. The amount of turnover, i.e. the amount of habitat area that is reallocated during the simulation time, was considerably influenced by the tax. A tax on turnover of 3 and 7 Euros per credit could, for most policy incentives, decrease the amount of turnover by approximately 25 respectively 50 percent. The predicted values are in the range between 0.7 and 2.5 of the total habitat area within 37 years (Fig. 4).

### *3.3. Economic changes*

Our simulation results show that, apart from small fluctuations, the market produces a stable supply of conservation credits $S^k$ that satisfy the demand $D^k$ during the whole simulation period (Fig. 5). The average benefits from alternative land use $\hat{B}^k$ are increasing during the simulation time, with two discontinuities in the years 2010 and 2020, that originate from the introduction of new economic boundary conditions as explained in the description of the economic model (sec. 2.3). To keep the supply $S^k$ constant when demand and net benefits of alternative land use are changing, the prices for credits are steadily increased during the simulation period, changing from approximately $4 - 5€/cr/yr$ to $11€/cr/yr$.

## 4. Discussion

### *4.1. Main results*

The results of the simulation show that a market-based policy with spatial and temporal incentives may effectively

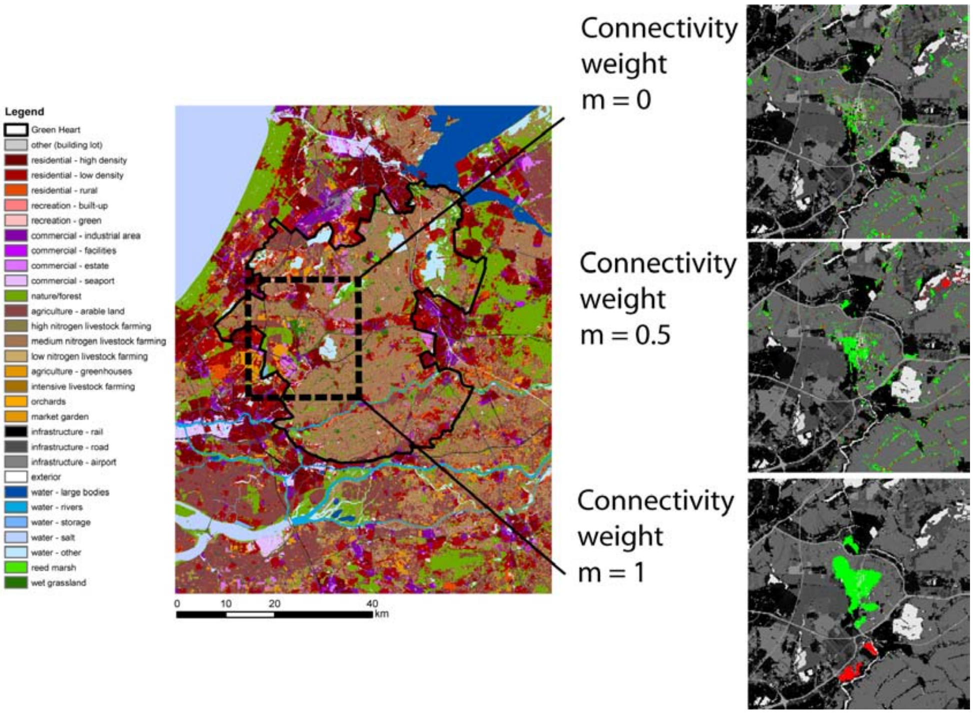

**Figure 3:** Effect of the spatial incentives: To the left, the resulting land use allocation of the base parameter combination $m = 0.5, l = 500, T = 3$ in 2040. The three maps to the right compare a subset of the map of the base incentive set (middle) with the results of simulations with a lower connectivity weight $m = 0$ (top) and a lower connectivity weight $m = 1$ (bottom). All other parameters were unchanged. It is clearly visible that the lower connectivity weight $m = 0$ leads to increased spread and habitats, and that the higher connectivity weight $m = 1$ leads to stronger clustering. Due to the fact that only a part of the area is shown, the perception of the absolute area of habitats is somewhat misleading. The incentive set with $m = 0$ maintains the lowest total area of habitats in the landscape, and the set with $m = 0$ the highest area.

control spatial connectivity and habitat turnover rates under economic change in the Randstadt region of the Netherlands. In particular the connectivity weight $m$, which creates incentives for clustering of habitats in the landscape, is found to be very effective for creating landscape structures that range from one big habitat cluster to very spread habitat configurations (Fig. 3).

The tax on reallocations of habitats was also found to be effective, however, even for the highest tax considered, the simulation still predicted a substantial change in land use within the simulation period of 37 years (Fig. 4). Depending on the incentives, up to one half of this turnover takes place during the first time step of the simulation. This is reasonable because the introduction of spatial incentives is likely to create larger land use changes while adjusting to the new incentives. Yet, even when targeting only area ($m = 0$), there is substantial pressure to reallocate the current habitats. This means that the simulation predicts that the same habitat area could be maintained at lower costs when reallocated elsewhere. It could well be that this pressure is in fact realistic, but area is not converted because of other regulations. Another reason, however, is that the model by (MNP, 2007) did not include these grasslands and marshlands before, and was not parameterized to predict land close to the initial spatial allocation in 2003. Therefore, some changes of land use during the transition from the empirical allocation in 2003 to the first simulation step in 2003.5 are to be expected. One may assume that real turnover rates would be slightly lower that in the simulation.

The economic indicators showed an increase of market prices from approximately $4-5€/cr/yr$ to $11€/cr/yr$ in the course of the 37 simulation years, which would translate into a price of approximately 6 to 16 $€/m^2/yr$ for conservation land use (Fig. 5). One part of this increase probably stems from the assumed increasing demand for housing and commercial areas in the simulations (see Appendix B.3). Another reason for the price increase is the assumed general increase of net economic benefits in the scenarios, which results in the need to adjust prices accordingly. We discuss the interpretation of this numbers in the next subsection. Generally, it can be concluded from the results that a functioning market will be able to maintain habitats in the region despite increasing pressure

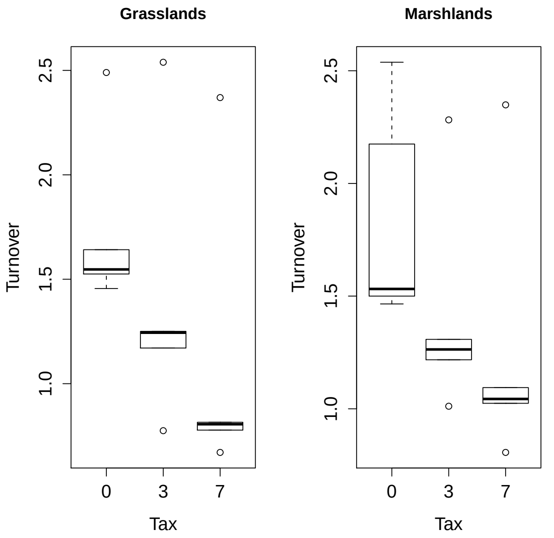

**Figure 4:** Effect of a tax on turnover: The box plots show the total amount of turnover during the simulation time in units of the total amount of the respective habitat type for the 22 of the 27 incentive sets. 5 of the parameter combination with the large connectivity radius $r = 1000$ were excluded from the analysis because market prices and therefore also the amount of habitats had not properly converged. This problem of convergence is caused by run-time limitations as explained in Appendix B.4

from other land use alternatives.

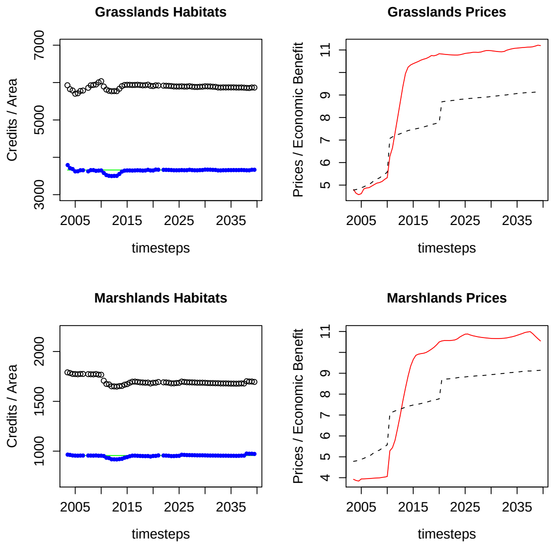

**Figure 5:** Economic indicators: The left column shows the development of credits supply $S^k$ (blue bullets), the credits demand $D^k$ (green line) and the area of habitats measured in units of the grid cell size (black circles) for grasslands (top) and marshlands (bottom) in the study region over time. The right collum shows the development of prices for credits $p^k$ in $€/cr/yr$ (solid lines) and the average allocated net economic benefit $\hat{B}_k$ per grid cell in $€/m^2/yr$ (dashed line) for grasslands (top) and marshlands (bottom) in the study region over time.

### *4.2. Interpretation and generality of the results*

Firstly, we would like to stress that a scenario-based simulation like the one used in this paper can only be interpreted as one possible trajectory of land use in the future. Regardless how much care is taken during preparation of the input, there is considerable uncertainty associated with the drivers of the model, e.g. economic development and population growth as well as with local uncertainties (i.e. local policy changes or changes of local land use due to changes of land owners or land users). It is difficult to say how likely any local trajectory is compared to others. Therefore, we discourage any quantitative or microscopic (i.e. small scale) interpretation of the simulation results. This, however, does not mean that the results cannot be used to derive conservation and policy recommendations for the study region. We believe that the macroscopic allocation of land use is realistic for the region and robust against small changes in the scenarios and local noise. The general findings regarding the effectiveness of incentives for clumping and connectivity, as well as relative importance of the different spatial factors are likely to be robust towards all these factors, too. Considerable care should be applied when interpreting economic indicators such as the net economic benefit $\hat{B}_i^k(t)$. Trends and rankings $\hat{B}_i^k(t)$ are likely to be credible, but the economic benefit $\hat{B}_i^k(t)$ as well as the predicted market prices should not be interpreted as Euro values.

The simulations show that the applied spatial incentives are effective in controlling the spatio-temporal allocation of conservation measures, but not that it is efficient to do so. The question of efficiency requires reliable measures of conservation benefits associated with this land use allocation, which is beyond the scope of this paper. Also, there may be additional economic benefits originating from ecosystem services such as water filtration or recreation that are not included in this analysis. In principle, however, a coupling of the market to an ecological model as in Hartig and Drechsler (2009) could be used to compare economic losses with the benefits for conservation, and apply either a cost-effectiveness or a cost-benefit analysis, depending on whether conservation benefits are available in the same unit as economic losses or not.

### *4.3. Implications for conservation policy*

The simulation shows that spatial and temporal incentives can be used for controlling the spatio-temporal configuration of conservation measures in a real world landscape. Previous studies such as Hartig and Drechsler (2009) suggest that, if conservation costs are spatially heterogeneous and the targeted species is sensitive to habitat fragmentation, spatial incentives robustly yield more conservation benefits at fixed costs than non-spatial incentives.

Our simulation predicts relatively high rates of turnover (reallocation of habitats) in the market. Ecologically, this could be problematic. Therefore, it seems advisable to combine spatial incentives with temporal incentives that limit the amount of landscape dynamics. The latter could e.g. be done with a tax, which was effective in our simulation results, or simply by limiting the legally permitted amount of turnover in the region. Used in this way, spatio-temporal incentives bear great potential for real world conservation markets. Given that current incentive mechanisms for farmers such as agri-environmental schemes rarely include any spatial components, it is important to gain more experience with this kind of conservation instruments. While our simulations show that spatial incentives create potential efficiency gains, there is still too little research about how the practical implementation of such a scheme can be organized, and how landowners would react to a spatially differentiated scheme in which rewards for conservation are not fixed and possibly different between neighbors.

## A. Data

### *A.1. Study area*

The study area is the Green Heart in the West of the Netherlands. This area is surrounded by the Randstad, a circle of cities consisting of Amsterdam, The Hague, Rotterdam and Utrecht and smaller adjacent cities. The Green Heart, as it name implies, is a relatively rural zone compared to its surroundings, with intensive dairy farming as dominant land use. The region, which has an extend of approximately $1870km^2$, was originally peat land and still fulfills and important role for species that depend on ecosystems like wet grasslands, reed marshes, peat bogs, and open water (resulting of peat harvest in former times). It also contains a number of important nature areas such as the Nieuwkoopse plassen and the Oostelijke Vechtplassen. We refer to the map of grid cells that belong to the Green Heart area, i.e. the zone in which conservation credits could be created, by the symbol $\Theta^{Zone}$ throughout this paper. $\Theta_i^{Zone}$ equals 1 if the cell belongs to the Green Heart area and 0 otherwise.

### *A.2. Habitat distribution maps*

One input of the model is the initial land use of 2003 on a $100m \times 100m$ grid. This map was created for the study of MNP (2007), and it did not contain marshlands and grasslands as individual land use types. The initial grass and marsh distribution is important because it influences the development of future land use through conversion costs, but also through the "attractive" effect of existing habitats that is caused by connectivity dependent incentives. We derived the current distribution of wet grasslands and reed marsh from Kramer et al. (2007) who provided a data set on the distribution of natural vegetation types in the Netherlands in 2004. For wet grassland, category 11 of this dataset (extensive grass) was overlayed with a map of the ground water table (map "gwt100" from MNP (2007)), selecting all grassland sites with high ground water level (Cat. I, II, III). For reed marsh we included all four reed land categories (cat. 80-83) from the data base. As the maps were provided on a $25m \times 25m$ resolution, they needed to be upscaled to the $100m \times 100m$ resolution and merged with the existing intial map of current land use from 2003. We used the same algorithm as it was used in MNP (2007) for the upscaling of the other land use types that were also upscaled and merged from existing $25m \times 25m$ maps. The initial habitat distributions on $25m \times 25m$ resolution are displayed in Fig. 6.

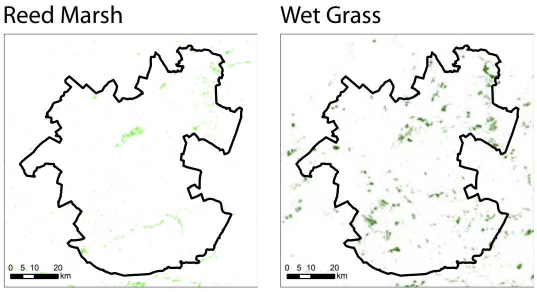

**Figure 6:** Habitat Distribution Maps: On the left, the current distribution of reed marshlands in the study area. On the right, the current distribution of wet grasslands. The borders of the Green Heart are displayed as a black line. The resolution of the maps is $25m \times 25m$.

### *A.3. Habitat potential maps*

The study area is heterogeneous with respect to the abiotic suitability for habitat restoration. Suitability indicators for reed marshes and wet grasslands based on soil type and hydrology (see Runhaar et al., 2005) were available as raster GIS maps. The theoretical range of the indicator was between 0 and 1000. The highest occurring value in the Netherlands was 99 for reed marshlands and 214 for wet grasslands. These maps are used to derive the areas that are in principle suitable for conversion. As we have no data on how costs scale with the potential, we assume the cost data we have was derived by converting sites with relatively high potential, and therefore applies for areas with $> 60$. Furthermore, we assume that areas with lower potential are too costly to convert and can therefore be excluded for conversion. The original potential maps and the suitable areas of values $> 60$, which we label by $\Theta^k$, are shown in Fig. 7.

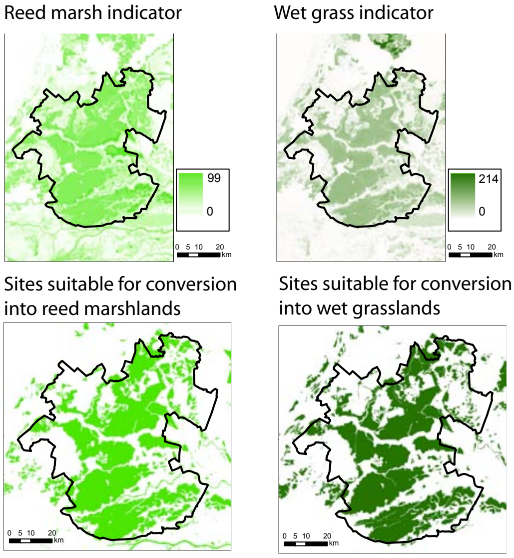

**Figure 7:** Habitat Potential Maps: On the left, the indicator of conversion potential into reed marshlands (top) and the areas with an indicator value $> 60$, that are potentially convertible (bottom). On the left, the indicator of conversion potential into wet grasslands (top) and the areas with an indicator value $> 60$, that are potentially convertible (bottom). As can be seen from the similarity of the maps, the necessary abiotic conditions for reed marshlands and wet grasslands are very similar. The borders of the Green Heart are displayed as a black line.

### *A.4. Conservation costs*

Costs, which arise for landowners from the maintenance and the recreation of habitats, are split into conversion costs and maintenance costs. Conversion costs occur when certain management actions have to be carried out to restore a habitat. For wet grasslands, possible measures include stopping drainage, top soil removal, repeated nutrient removal management (e.g. mowing, removing plant material) and sod cutting. Measures for reed marsh encompass: raising the groundwater table, superficial inundation, removing top soil or dredging (Bal et al., 2001).

Maintenance costs $M^k$ are independent of the former use and encompass all costs that arise from the continuous management of the habitat types. Maintenance costs originate e.g. from the need to prevent an increase in nutrients (mowing and removal of mown material, grazing, local sod cutting) or from the need to prevent succession into old reed and marsh forest (e.g. mowing and removal of biomass) (Bal et al., 2001; de Jong et al., 2007).

We use cost data from De Koeijer et al. (2008) for these habitat types, classified according to soil type (e.g. peat soil or river clay), however, the differences between soil types were small compared to other prices in the model, and we therefore used a rounded average for conversion and maintenance costs (Table 1).

There was no information available on how one-time costs were transformed into yearly costs for the parameters that were used from (MNP, 2007). Therefore, we assumed that market rates of discounting were used, and we transformed one-time conversion costs of the habitat types accordingly at a discount rate of 5% with an infinite time horizon.

Additionally, we assumed that maintenance costs are optimal costs that could be realized by a supplier who specializes on the provision of conservation. For a farmer who only occasionally engages in conservation on a small scale, they may be considerably higher. Therefore, we added a random component, drawn from a uniform distribution between 0 and 1, on top of the maintenance costs of each grid cell.

| Type | Costs [€$/m^2/yr$] |
|---|---|
| Mean conversion costs: | |
| Grass | 1 |
| Marsh | 0.8 |
| Mean maintenance costs: | |
| Grass | $0.55 + \mathbf{unif}[0,1]$ |
| Marsh | $0.46 + \mathbf{unif}[0,1]$ |

**Table 1:** Mean conversion and maintenance costs.

## B. Model details

### *B.1. DMS software and source code*

The study is implemented in the modelling framework Geo Data and Model Server(GeoDMS). The core of the GeoDMS software is a set of compiled C++ functions that enable operations on GIS data. Models using these functions are defined in one or several configuration files that use a GeoDMS specific syntax. The GeoDMS reads these configuration files and executes the calculations with the core libraries. The GeoDMS software is distributed by the company object vision under the terms of the GNU General Public License. Sourcecode of the software can be found at http://sourceforge.net/ projects/geodms/. Installers of the software and documentation can be found at http://www.objectvision.nl/Geodms/. The configuration files of the model including the parts that were used from existing models, in particular of MNP (2007) is available at www.ecotrade.ufz.de/casestudy.html. Table 2 shows a list of the implemented land use types.

### *B.2. Details of the economic base model*

The study of (MNP, 2007) is based on the land use scanner model (Hilferink and Rietveld, 1999; Schotten et al., 2001; Eppink et al., 2008; Koomen et al., 2008). It uses the discrete version of this model that is described in (Koomen et al., 2008). (MNP, 2007) parameterized the land use scanner model for the prediction of land use change in the Netherlands for the next 40 years. In the next subsection, we briefly summarize the key assumptions of this parametrization, which was used as a base for the dynamic scenarios in this paper.

| Number | Land Use Type |
|---|---|
| 0 | residential - high density |
| 1 | residential - low density |
| 2 | residential - rural |
| 3 | recreation - built-up |
| 4 | recreational green |
| 5 | commercial - industrial area |
| 6 | commercial - facilities |
| 7 | commericial - estate |
| 8 | commercial - seeport |
| 9 | nature/forest |
| 10 | agriculture - arable land |
| 11 | agriculture - high nitrogen livestock farming |
| 12 | agriculture -medium nitrogen livestock farming |
| 13 | agriculture - low nitrogen livestock farming |
| 14 | agriculture - greenhouse |
| 15 | agriculture - intensive livestock farming |
| 16 | agriculture - orchards |
| 17 | agriculture - nursery |
| 18 | infrastructure - rail |
| 19 | infrastructure - roads |
| 20 | infrastructure - airports |
| 21 | other - building lot |
| 22 | exterior |
| 23 | water - large bodies |
| 24 | water - rivers |
| 25 | water - storage |
| 26 | water - saltwater |
| 27 | water - other waters |
| 28 | reed marsh |
| 29 | wet grassland |

**Table 2:** Land use types.

### B.3. Trend Scenario

The interpolation of economic conditions in our simulation uses the high pressure trend scenario from (MNP, 2007). This scenario assumes a yearly economic growth of $2,1\%$ and 20 million inhabitants for the Netherlands in 2040. The scenarios were constructed with local authorities of the provinces of the Netherlands, in particular for the hedonic suitabilities $H_i^k(t)$ of sites for residential areas, commercial areas and greenhouses in 2010. Between 2010 and 2040, it was estimated that build-up area would increase by 190.000 ha. The highest increase is expected in South Holland, North Brabant and North Holland (the case study region covers areas from South and North Holland and lies in the North of North Brabant). Additionally, it is expected that a major network of ecological reserves, the ecological main structure (ecologische hoofdstructuur), will be completed by 2020. Therefore, up to 2020 it is expected that additional area will be dedicated for conservation and no more thereafter. The increases in those land use types are expected to lead to a decrease in agricultural area around 260.000 ha, which was considered in the constraints.

### B.4. Real time steps and price adjustment

If economic conditions change, the price adjustment (eq. 9) may not suffice to correct the market price in one time step. The undershooting or overshooting of endpoints that would result from a wrong price, however, may create a different landscape configuration than the landscape configuration that would arise from equilibrium development. The reason is that, in an equilibrium situation, it is always more expensive to create new patches than to keep the old ones. If the price for a certain conservation type is too low, however, a lot of patches may be lost, with the result that they are costly to restore in the next step and might therefore not be chosen. Therefore, we implemented a number of intermediate steps to make sure that the prices $p^k$ converge and the supply of endpoints $S^k$ meets the demand $D^k$. We call these intermediate time steps iterations (Fig. 8). At each iteration, the market price is adjusted and the allocation of all land use types is recalculated. Also, the spatial information of the existing habitats, which is necessary to calculated the conservation credits, is taken from the last landscape configuration of the last iteration. This mechanism may be viewed as an exchange of information about the current state of landowners decisions and ensures faster convergence to a spatial pattern (Hartig and Drechsler, in press). The calculation of conversion costs always refers to the last real time step. Thus, the difference between iterations and real time steps is that iterations are used to adjust the market price, but conversion costs resulting from the existing landscape configuration are obtained from the last real time step.

At each time step, the difference between supply and fixed demand of conservation credits $\Delta$ is calculated according to eq. 7, and the price is adjusted upwards if there is too little credit supply and downwards if there is too much credit supply. If the function that gives the marginal costs for additional conservation was perfectly known, and in particular if marginal costs were constant, we could simply calculate the right price at which the supply meets the fixed demand. But because the "yield" of a patch, i.e. the amount of credits produced, is not fixed, there is no straightforward way to predict the right price. Therefore, we adjust the price stepwise to reach convergence.

For fast convergence, the price adjustment should depend

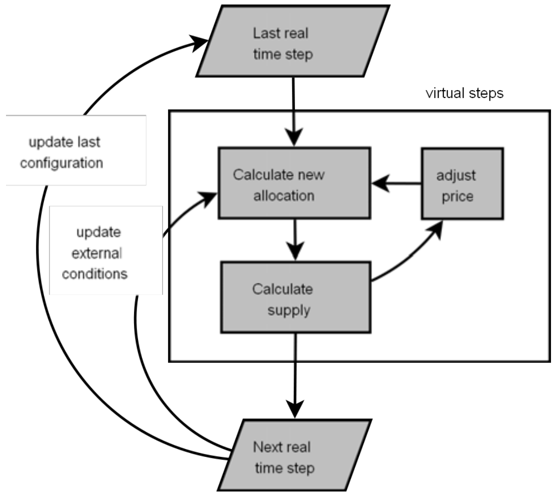

**Figure 8:** Flow chart of the processes within one time step.

on the lack of ecopoints $\Delta S$, such that a larger $\Delta S$ results in stronger adjustments. On the other hand, if price adjustment steps are too large, prices may overshoot and the supply may start to fluctuate. To solve this problem, it makes sense to limit the maximum range of the price adjustment function. We chose a sigmoid function

$$\Delta P^k = \frac{\chi \cdot sign(\Delta S^k)}{1+e^{-\alpha(\Delta S^k - \tau\cdot\alpha)}} - \frac{\chi \cdot sign(\Delta S^k)}{1+e^{-\alpha(\tau\cdot\alpha)}} \qquad (9)$$

where $\Delta P$ is price adjustment, $\Delta S$ is the difference between demand and supply, $\phi$ determines the strength of the price adjustment, $\alpha$ is the sensitivity of the sigmoid function, and $\Theta$ determines whether the function starts in the convex or the concave area. We used the following parameters for eq. 9: $\chi = 1.5$, $\alpha = 3$, $\tau = 0.05$ .

## References

Bal, D., Beije, H., Fellinger, M., Haveman, R., Van Opstal, A., Van Zadelhoff, F., 2001. Handboek Natuurdoeltypen. Expertisecentrum LNV. Dutch Ministry of Agriculture, Environment and Fisheries, Wageningen.

Chomitz, K. M., 2004. Transferable development rights and forest protection: An exploratory analysis. Int. Regional. Sci. Rev. 27 (3), 348–373.
doi: 10.1177/0160017604266030

de Jong, J., Bouwma, I., van Wijk, M., 2007. Beheerskosten van Natura 2000-gebieden. Tech. rep., Werkdocument / Wettelijke Onderzoekstaken Natuur & Milieu: 56. Wettelijke Onderzoekstaken Natuur & Milieu, Wageningen.
`http://library.wur.nl/way/bestanden/clc/1870078.pdf`

De Koeijer, T., Van Bommel, K., Clement, J., Groeneveld, R., De Jong, J., Oltmer, K., Reijnen, M., Wijk, M. V., 2008. Kosteneffectiviteit van de terrestrische ecologische hoofdstructuur. Tech. rep., Wettelijke Onderzoekstaken Natuur & Milieu: 73, Wageningen.
`http://library.wur.nl/way/bestanden/clc/1880669.pdf`

Drechsler, M., 2009. Predicting metapopulation lifetime from macroscopic network properties. Math. Biosci. 218 (1), 59 – 71.
doi: 10.1016/j.mbs.2008.12.004

Drechsler, M., Hartig, F., submitted. tradable permit dynamics, manuscript to JEEM.

Drechsler, M., Wätzold, F., 2009. Applying tradable permits to biodiversity conservation: Effects of space-dependent conservation benefits and cost heterogeneity on habitat allocation. Ecol. Econ. 68 (4), 1083–1092.
doi: doi:10.1016/j.ecolecon.2008.07.019

Drechsler, M., Wätzold, F., Johst, K., Bergmann, H., Settele, J., 2007. A model-based approach for designing cost-effective compensation payments for conservation of endangered species in real landscapes. Biol. Conserv. 140 (1-2), 174–186.
doi: 10.1016/j.biocon.2007.08.013

Engel, S., Pagiola, S., Wunder, S., 2008. Designing payments for environmental services in theory and practice: An overview of the issues. Ecol. Econ. 65 (4), 663–674.
doi: 10.1016/j.ecolecon.2008.03.011

Eppink, F. V., Rietveld, P., van den Bergh, J. C., Vermaat, J. E., Wassen, M. J., Hilferink, M., 2008. Internalising the costs of fragmentation and nutrient deposition in spatial planning: Extending a decision support tool for the Netherlands. Land Use Policy 25 (4), 563–578.

Fahrig, L., 2002. Effect of habitat fragmentation on the extinction threshold: A synthesis. Ecol. Appl. 12 (2), 346–353.

Hanski, I., 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87 (2), 209–219.

Hartig, F., Drechsler, M., 2009. Smart spatial incentives for market-based conservation. Biol. Conserv. 142 (4), 779–788, http://arxiv.org/abs/0809.0228.
doi: 10.1016/j.biocon.2008.12.014

Hartig, F., Drechsler, M., in press. Stay by thy neighbor? Social organization determines the efficiency of biodiversity markets with spatial incentives. Ecol. Complex. http://arxiv.org/abs/0808.0111.
doi: 10.1016/j.ecocom.2009.07.001

Hilferink, M., Rietveld, P., 1999. LAND USE SCANNER: An integrated GIS based model for long term projections of land use in urban and rural areas. Journal of Geographical Systems 1 (2), 155–177.

Jack, B. K., Kousky, C., Sims, K. R. E., 2008. Designing payments for ecosystem services: Lessons from previous experience with incentive-based mechanisms. Proc. Natl. Acad. Sci. U. S. A. 105 (28), 9465–9470.
doi: 10.1073/pnas.0705503104

Koomen, E., Loonen, W., Hilferink, M., 2008. Climate-Change Adaptations in Land-Use Planning; A Scenario-Based Approach. The European Information Society, 261–282.
doi: 10.1007/978-3-540-78946-8

Kramer, H., Hazeu, G. W., Clement, J., 2007. Basiskaart Natuur 2004. Vervaardiging van een landsdekkend basisbestand terrestrische natuur in Nederland. WOt-werkdocument 40, Wettelijke Onderzoekstaken Natuur & Milieu, Wageningen UR, Wageningen.

Kuhn, H. W., Tucker, A. W., 1951. Nonlinear programming. In: Proceedings of the Second Berkeley Symposium on Mathematical Statistics and Probability. University of California Press, pp. 481–492.

Latacz-Lohmann, U., Van der Hamsvoort, C. P. C. M., 1998. Auctions as a means of creating a market for public goods from agriculture. J. Agr. Econ. 49 (3), 334–345.

MNP, 2007. Nederland later. Tweede duurzaamheidsverkenning, deel fysieke leefomgeving nederland. Tech. rep., Netherlands Environmental Assessment Agency.
`http://www.mnp.nl/nl/publicaties/2007/Duurzaamheidsverkenning2Nede`

Panayotou, T., 1994. Conservation of biodiversity and economic development: The concept of transferable development rights. Environ. Resour. Econ. 4 (1), 91–110.
doi: 10.1007/BF00691934

Polasky, S., 2006. You can't always get what you want: Conservation planning with feedback effects. P. Natl. Acad. Sci. Usa. 103 (14),

5245–5246.
doi: 10.1073/pnas.0601348103

Polasky, S., 2008. Why conservation planning needs socioeconomic data. Proc. Natl. Acad. Sci. U. S. A. 105 (18), 6505–6506.
doi: 10.1073/pnas.0802815105

Runhaar, J., Clement, J., Jansen, P., Hennekens, S., Weeda, E., Wamelink, W., Schouwenberg, E., 2005. Hotspots floristische biodiversiteit. Tech. rep., Wettelijke Onderzoekstaken Natuur & Milieu, WOt-rapport 9, Wageningen.
`http://library.wur.nl/way/bestanden/clc/1802448.pdf`

Salzman, J., 2005. Creating markets for ecosystem services: Notes from the field. New York U. Law Rev. 80 (3), 870–961.

Salzman, J., Ruhl, J. B., 2000. Currencies and the commodification of environmental law. Stanford Law Rev. 53 (3), 607–694.

Saunders, D. A., Hobbs, R. J., Margules, C. R., 1991. Biological consequences of ecosystem fragmentation: A review. Conserv. Biol. 5 (1), 18–32.
doi: 10.1111/j.1523-1739.1991.tb00384.x

Schotten, K., Goetgeluk, R., Hilferink, M., Rietveld, P., Scholten, H., 2001. Residential Construction, Land Use and the Environment. Simulations for the Netherlands Using a GIS-Based Land Use Model. Environmental Modeling and Assessment 6 (2), 133–143.

Weitzman, M. L., 1974. Prices vs quantities. Rev. Econ. Stud. 41 (128), 477–491.

Wissel, S., Wätzold, F., 2008. Applying tradable permits to biodiversity conservation: A conceptual analysis of trading rules. UFZ Discussion Paper 7/2008.

Wunder, S., 2007. The efficiency of payments for environmental services in tropical conservation. Conserv. Biol. 21 (1), 48–58.
doi: 10.1111/j.1523-1739.2006.00559.x

The following second author publications, partly in preparation, have been produced in connection with this PhD:

### Paper VI

Guy Pe'er, Florian Hartig, Martin Drechsler, Josef Settele and Karin Frank

**The dynamic fingerprint as a tool for adjusting disturbance regimes to ecosystems needs in human-dominated landscapes**

submitted

### Paper VII

Martin Drechsler and Florian Hartig

**Conserving biodiversity with tradable permits in the face of economic dynamics and habitat restoration time lags**

in preparation

### Paper VIII

Frank Wätzold, Martin Drechsler, Florian Hartig, Silvia Wissel

**Applying tradable permits to biodiversity conservation: Design issues, modelling and policies**

Book chapter, submitted

Chapter 4

# Conclusion and Outlook

## 4.1 Main results

Below, we list the main findings of our research. In the rest of the chapter, we explain the relevance of each point in more detail, and discuss implications for the research questions raised in the introduction. Our main results are:

1. **Trade-offs between species are sensitive to time preferences:** In paper 1, we showed that multi-species objective functions for survival between species are sensitive to the applied time horizon.

2. **Spatial incentives in conservation markets allow to control the spatial network properties:** In paper 4 and paper 5, we showed that simple spatial incentives allow to control the spatial allocation of habitats emerging from a conservation market. In paper 2, we showed that these incentives can considerably increase the efficiency of market-based policies, even when they do not capture the full complexity of ecological processes on the landscape scale. In paper 3, we developed an experimental setup in form of a network game to examine whether real players would take decisions similar to the predictions from simulation studies.

3. **Temporal incentives are crucial for the efficiency of conservation markets:** In paper 2, we showed that the effectiveness of spatial incentives is highly dependent on the underlying dynamics of conservation costs. The reason is that economic dynamics together with spatial incentives determine the amount of habitat turnover in the landscape. In paper 5 we showed how spatial and temporal incentives can be combined to control the spatio-temporal allocation of habitats in a real landscape.

## 4.2 Discussion of the results

Our research concentrated on three questions: How can trade-offs between different species be quantified? How can spatial processes, in particular metapopulation processes and the control of landscape fragmentation, be included in market-based conservation policies? Finally, how do ecological and economic dynamics affect each other, and how can conservation markets account for dynamical processes such as time lags of restoration measures or succession? In the following, we discuss the results of our research in the light of these three questions.

### 4.2.1 Time preferences and species trade-offs

Including trade-offs between multiple species survival into conservation policies requires the choice of an objective function that transforms survival probabilities of multiple species into one single value. Different forms of objective functions have been used in the literature, some of which maximize the expected number of surviving species (additive functions), whereas others also emphasize an even distribution of survival probabilities among species (multiplicative functions or weighted additive functions). In paper 1, we showed that objectives using additive functions may be strongly affected by the time horizon when at least one of the following two assumptions is fulfilled: (a) the functional relation between budget expenditures and survival is sufficiently concave; or (b) the multi-species objective function puts a sufficiently strong weight on even survival probabilities and the relationship between costs and survival is concave, linear, or sufficiently weakly convex. For our simple case of two species, conservation decisions based on such functions change drastically when the time horizon crosses some critical value.

We concluded that the influence of time preferences on conservation decisions has not sufficiently been acknowledged in the past. Time preferences are particularly important for dynamical problems such as conservation markets, but they may also impact when external dynamic drivers such as climate and global change are present. Thus, time preferences should be selected with care, and their influence should be analyzed and communicated when calculating and presenting conservation recommendations.

### 4.2.2 Spatial issues

The value of a habitat patch typically depends on the land use in its vicinity. The reason is that, for many endangered species, not only the absolute loss of habitat area, but also habitat fragmentation is a major cause of population decline (compare e.g. Saunders et al., 1991; Fahrig, 2002). It is therefore a concern that most existing market schemes base their evaluation on the quality and size of the local site only without considering its surroundings.

### Including spatial trade-offs

One possibility to account for spatial processes is to explicitly include spatial trade-offs into the market values of conservation measures. In such a case, the potential benefit of a conservation measure may change depending on the conservation measures that are undertaken by landowners in the surrounding. A perfect market should then automatically choose the best spatial allocation of conservation measures given the opportunity costs of all market participants. We showed in paper 2 that spatial incentives can in fact considerably increase the efficiency of conservation measures, and we showed in paper 5 that these incentives would also be effective in real landscapes.

There is, however, the concern that market participants may react suboptimally towards incentives, which may decrease the efficiency of conservation measures. In paper 4, we examined three problems:

- **Incomplete information**: Landowners may not have full information about the costs and incentives of their neighbors. Therefore, their decisions may be different to the optimal decision under full information.
- **Externalities**: A spatial dependence of the value of conservation measures creates a spatial externality between landowners. Ideally, market participants could resolve this situation through bargaining, but under incomplete information this is likely to fail.
- **Complexity**: Spatially interdependent payments create a complicated optimization problem. If agents' capabilities to optimize their actions are limited, their decisions may be suboptimal.

Thus, the need to consider a system of interacting individual landowners creates a trade-off: Ecological accuracy calls for a metric that is complex enough to capture all relevant spatial ecological processes, but experience or estimates from agent-based models may suggest a simpler metric that avoids losses from suboptimal individual decisions. If spatial trade-offs are considered too complicated to implement, zoning may be a compromise between top-down planning and market-approaches. Zoning means that compensation measures are only allowed in a certain zone. That way, spatial trade-offs are not included in the market incentives, but regulated top-down by the conservation authority. The market only helps to reveal the most cost-effective allocation within the zones (Fig. 4.1).

While agent-based models can aid to understand the mechanisms in a spatial conservation market, only real world experiments can give final certainty about how individuals are going to react to certain incentive systems. In paper 3, we presented a multi-player network game that can be used to conduct virtual experiments of conservation markets with spatial certificates. In the game, players own land parcels in a virtual landscape and are subject to changing benefits from agriculture and incentives from a spatial tradable permit scheme. The latest version (version 1.1) includes the possibility to record and

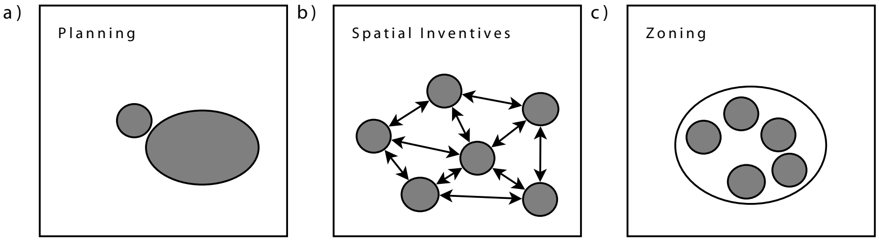

**Figure 4.1:** Options to control space: a) A planning approach means full top-down control of the conservation measure b) A market with explicit spatial incentives c) Zoning. Here, the large scale spatial allocation is fixed top down, but within a zone market participants compete for the conservation measure.

analyze the decisions of the players. The software may be used to test the effectiveness and acceptance of different spatial incentive mechanisms.

### 4.2.3 Dynamics

Unlike a static optimization, which results in a static plan for a certain region, markets are by their nature dynamic. While markets conditions may change fast, ecosystems recover at a much smaller pace. Many conservation measures develop their value only after years or decades. Thus, it is crucial to to analyze and control the interplay between economic dynamics and ecological dynamics in conservation markets.

We found that the conservation of favorable landscape dynamics is vital for many species, and neglecting landscape dynamics may lead to severe problems for the effectiveness of conservation measures. Without controlling the dynamics of conservation markets, i.e. the temporal change of conservation measures, those dynamics would most probably be dominated by economic drivers, which may not be beneficial for species. As shown in paper 2, optimal conservation incentives in a conservation market depend also on the underlying economic dynamics. Therefore, it seems advisable to support spatial incentive systems by mechanisms that limit or control landscape dynamics. In paper 5, we showed that a combination of spatial and temporal incentives may be used to control fragmentation and landscape dynamics in a real landscape at the same time.

## 4.3 Future research

### 4.3.1 The relevance of time preferences

We believe that the findings of paper 1 reflect a much broader problem in the environmental debate that has not yet been sufficiently addressed by conservation research: For most environmental problems, time preferences have a considerable influence on the "optimal" decision. Is climate change a major threat or not? The answer to this question may be very different depending on the time horizon that is applied (Nordhaus, 2007). Most scientists who argue about responses to environmental problems implicitly use certain time preferences. These preferences are often not made explicit as a normative choice, possibly for reasons of being unaware of the importance of these preferences, but maybe also because personal convictions are so dominant that they are hardly questioned. We believe that there are two major areas for future research. First of all, it is important to study and communicate the impact of time preferences for modelling and optimization studies. Secondly, we need more research on time preferences for global resources such as biodiversity. Nordhaus (2007) for example criticized the Stern report for its low discount rate on the consequences of climate change (Stern et al., 2006). Typical economic discount rates for capital are around 6% per year, corresponding to a time horizon of approximately 17 years. This would, in consequence, mean that the long-term persistence of biodiversity is practically worthless. There is, however, a lot of evidence that human preferences for conservation are characterized by much longer time preferences. Conservationists usually do not discount the projected presence of a species at 6% per year. We have to find ways to include such long-term preferences systematically in our models if we want to produce informed advice for environmental policy.

### 4.3.2 The need for experiments that include socioeconomic data

Market-based conservation is characterized by one major idea: Instead of fixing resource consumption by top-down control, landowners should experience the positive and negative external effects of their actions and thereby automatically only use natural resources when the benefits of their use are higher than the societal costs. Yet, we have stressed throughout our research that such an internalization is characterized by a trade-off. The more detailed we assess external effects of land use in a market, the more complicated becomes the market for the market participants, and also the more costly for the regulating authority. In recent decades, large technical progress was made in understanding ecosystems as well as having the opportunity for applying this knowledge on a large scale by means of computers, GIS systems and satellite data. Very little, however, is understood about the underlying socio-economics dynamics of land use change. In particular, we are lacking data on costs, but also on motives of players involved in conservation schemes (Polasky, 2008). Additionally, there are barely any comprehensive studies that compare the effectiveness of different market forms and different incentive mechanisms of different complexity. Such large studies that include all major variables as well as more practical experiments are urgently needed for the design of future conservation markets.

### 4.3.3 Finding ecological-economic "surrogates"

Ecological research has assigned great efforts to finding indicators or surrogates that provide an easy way of relating easily measurable quantities to the biodiversity and the ecological value of a site. Examples of this include taxa-based surrogates such as flagship, umbrella and keystone species (Simberloff, 1998; Caro and O'Doherty, 1999; Halme et al., 2009), but also indicators based on habitat models that relate abiotic conditions of a site to the presence of species (Guisan and Thuiller, 2005), or indicators based on properties of the habitat network (Frank and Wissel, 2002; Drechsler, 2009). Practically all systematic conservation planning relies on the use of some indicators or surrogates, because an exact analysis of sites in a conservation planning process of a large region is virtually impossible (Margules and Pressey, 2000; Cabeza and Moilanen, 2001).

In market-based conservation instruments, the metric that calculates the "biodiversity market value" of a site is, on the first glance, based on the same idea as indicators of biodiversity. We want a metric that translates easily measurable quantities into an incentive for landowners. Clearly, research about ecological indicators and surrogates is very related to this question and provides valuable information for choosing appropriate metrics. Simply translating existing ecological surrogates to metrics for biodiversity markets, however, may be short-sighted, because this completely neglects the socio-economic system that reacts to the incentives created by the scheme (paper 4). Besides ecological factors, socio-economic factors such as transaction costs, externalities, social organization or equity may be equally important for choosing metrics for incentive-based conservation schemes. In paper 2, for example, we showed that optimal incentives depend on the species, but also on the spatio-temporal distribution of conservation costs. Therefore, incentive-based conservation approaches need "ecological-economic surrogates", that establish a correlation between incentives and conservation success in a particular socio-economic setting. The results from this dissertation show that there is further need for studies that combine ecological and economic indicators to find out which economic incentive schemes work for which combinations of ecological and economic systems.

# Bibliography

Ando, A., Camm, J., Polasky, S., Solow, A., 1998. Species distributions, land values, and efficient conservation. Science 279 (5359), 2126–2128.
doi: 10.1126/science.279.5359.2126

Andren, H., 1994. Effects Of Habitat Fragmentation On Birds And Mammals In Landscapes With Different Proportions Of Suitable Habitat - A Review. Oikos 71 (3), 355–366.

Balmford, A., Bruner, A., Cooper, P., Costanza, R., Farber, S., Green, R. E., Jenkins, M., Jefferiss, P., Jessamy, V., Madden, J., Munro, K., Myers, N., Naeem, S., Paavola, J., Rayment, M., Rosendo, S., Roughgarden, J., Trumper, K., Turner, R. K., 2002. Economic Reasons for Conserving Wild Nature. Science 297 (5583), 950–953.
doi: 10.1126/science.1073947

Begon, M., Townsend, C. R., Harper, J. L., 2006. Ecology : from individuals to ecosystems, 4th Edition. Blackwell Publishing Inc.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F., Nystrom, M., 2003. Reserves, resilience and dynamic landscapes. Ambio 32 (6), 389–396.
doi: 10.1639

Bottrill, M. C., Joseph, L. N., Carwardine, J., Bode, M., Cook, C., Game, E. T., Grantham, H., Kark, S., Linke, S., McDonald-Madden, E., Pressey, R. L., Walker, S., Wilson, K. A., Possingham, H. P., 2008. Is conservation triage just smart decision making? Trends in Ecology & Evolution 23 (12), 649–654.
doi: doi:10.1016/j.tree.2008.07.007

Cabeza, M., Moilanen, A., 2001. Design of reserve networks and the persistence of biodiversity. Trends in Ecology & Evolution 16 (5), 242–248.

Caro, T. M., O'Doherty, G., 1999. On the use of surrogate species in conservation biology. Conservation Biology 13 (4), 805–814.

Chapin III, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C., Diaz, S., 2000. Consequences of changing biodiversity. Nature 405 (6783), 234–242.
doi: 10.1038/35012241

Chomitz, K. M., 2004. Transferable development rights and forest protection: An exploratory analysis. Int. Regional. Sci. Rev. 27 (3), 348–373.
doi: 10.1177/0160017604266030

Coase, R. H., 1960. The problem of social cost. Journal Of Law & Economics 3 (OCT), 1–44.

Coggan, A., Whitten, S. M., 2005. Market Based Instruments (MBIs) in Australia: What are they, important issues to consider and some applications to date. Tech. rep., CSIRO, accessed 29.11.2008.
`http://www.ecosystemservicesproject.org/html/publications/docs/Intro_to_MBIs_2005.pdf`

Connell, J. H., 1978. Diversity in Tropical Rain Forests and Coral Reefs. Science 199 (4335), 1302–1310.
doi: 10.1126/science.199.4335.1302

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R. G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387 (6630), 253–260.
doi: 10.1038/387253a0

Dickman, R., Vidigal, R., 2002. Quasi-stationary distributions for stochastic processes with an absorbing state. Journal of Physics A: Mathematical and General 35 (5), 1147–1166.

Drechsler, M., 1994. Stochstische Modelle zu den Überlebenschancen von Metapopulationen. Verlak Shaker.

Drechsler, M., 2009. Predicting metapopulation lifetime from macroscopic network properties. Math. Biosci. 218 (1), 59 – 71.
doi: 10.1016/j.mbs.2008.12.004

Drechsler, M., Wätzold, F., 2009. Applying tradable permits to biodiversity conservation: Effects of space-dependent conservation benefits and cost heterogeneity on habitat allocation. Ecol. Econ. 68 (4), 1083–1092.
doi: doi:10.1016/j.ecolecon.2008.07.019

Drechsler, M., Wätzold, F., Johst, K., Bergmann, H., Settele, J., 2007. A model-based approach for designing cost-effective compensation payments for conservation of endangered species in real landscapes. Biol. Conserv. 140 (1-2), 174–186.
doi: 10.1016/j.biocon.2007.08.013

Engel, S., Pagiola, S., Wunder, S., 2008. Designing payments for environmental services in theory and practice: An overview of the issues. Ecol. Econ. 65 (4), 663–674.
doi: 10.1016/j.ecolecon.2008.03.011

Fahrig, L., 2002. Effect of habitat fragmentation on the extinction threshold: A synthesis. Ecol. Appl. 12 (2), 346–353.

Faith, D. P., Walker, P. A., 1996. Integrating conservation and development: effective trade-offs between biodiversity and cost in the selection of protected areas. Biodivers. Conserv. 5 (4), 431–446.
doi: 10.1007/BF00056389

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C. S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annu. Rev. Ecol. Evol. S 35, 557–581.
doi: 10.1146/annurev.ecolsys.35.021103.105711

Fox, J., Nino-Murcia, A., 2005. Status of species conservation banking in the United States. Conserv. Biol. 19 (4), 996–1007.
doi: 10.1111/j.1523-1739.2005.00231.x

Frank, K., Wissel, C., 2002. A formula for the mean lifetime of metapopulations in heterogeneous landscapes. Am. Nat. 159 (5), 530–552.

Frederick, S., Loewenstein, G., O'Donoghue, T., 2002. Time discounting and time preference: A critical review. J. Econ. Lit. 40 (2), 351–401.

Frey, B. S., 1992. Tertium Datur - Pricing, Regulating And Intrinsic Motivation. Kyklos 45 (2), 161–184.

Grime, J. P., 1973. Competitive Exclusion in Herbaceous Vegetation. Nature 242 (5396), 344–347.
doi: 10.1038/242344a0

Grimm, V., Railsback, S., 2005. Individual-Based Modeling and Ecology. Princeton University Press.

Grimm, V., Wissel, C., 2004. The intrinsic mean time to extinction: A unifying approach to analysing persistence and viability of populations. Oikos 105 (3), 501–511.
doi: 10.1111/j.0030-1299.2004.12606.x

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8 (9), 993–1009.
doi: 10.1111/j.1461-0248.2005.00792.x

Halme, P., Mönkkönen, M., Kotiaho, J. S., Ylisirniö, A.-L., Markkanen, A., 2009. Quantifying the Indicator Power of an Indicator Species. Conservation Biology 23 (4), 1008–1016.

Hanski, I., 1998. Metapopulation dynamics. Nature 396, 41–49.
doi: 10.1038/23876

Hanski, I., 1999a. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87 (2), 209–219.

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

Hanski, I., Gilpin, M., 1991. Metapopulation Dynamics - Brief-History And Conceptual Domain. Biological Journal Of The Linnean Society 42 (1-2), 3–16.

Hanski, I., Moilanen, A., Gyllenberg, M., 1996. Minimum viable metapopulation size. Am. Nat. 147 (4), 527–541.

Hanski, I., Ovaskainen, O., 2000. The metapopulation capacity of a fragmented landscape. Nature 404 (6779), 755–758.
doi: 10.1038/35008063

Hanski, I., Ovaskainen, O., 2002. Extinction debt at extinction threshold. Conserv. Biol. 16, 666–673.

Hardin, G., 1968. The Tragedy of the Commons. Science 162 (3859), 1243–1248.
doi: 10.1126/science.162.3859.1243

Heal, G., 2007. Discounting: A review of the basic economics. U. Chicago Law Rev. 74 (1), 59–77.

Henderson, N., Sutherland, W. J., 1996. Two truths about discounting and their environmental consequences. Trends in Ecology & Evolution 11 (12), 527–528.
doi: 10.1016/S0169-5347(96)20083-7

Hobbs, R. J., Huenneke, L. F., 1992. Disturbance, diversity, and invasion - implications for conservations. Conserv. Biol. 6 (3), 324–337.

Holmes, E. E., Lewis, M. A., Banks, J. E., Veit, R. R., 1994. Partial Differential Equations in Ecology: Spatial Interactions and Population Dynamics. Ecology 75 (1), 17–29.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A. J., Vandermeer, J., Wardle, D. A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75 (1), 3–35.

Jack, B. K., Kousky, C., Sims, K. R. E., 2008. Designing payments for ecosystem services: Lessons from previous experience with incentive-based mechanisms. Proc. Natl. Acad. Sci. U. S. A. 105 (28), 9465–9470.
doi: 10.1073/pnas.0705503104

Johst, K., Brandl, R., Eber, S., 2002. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. Oikos 98 (2), 263–270.

Johst, K., Drechsler, M., 2003. Are spatially correlated or uncorrelated disturbance regimes better for the survival of species? Oikos 103 (3), 449–456.

Kallimanis, A. S., Kunin, W. E., Halley, J. M., Sgardelis, S. P., 2005. Metapopulation extinction risk under spatially autocorrelated disturbance. Conservation Biology 19 (2), 534–546.

Konvicka, M., Benes, J., Cizek, O., Kopecek, F., Konvicka, O., Vitaz, L., 2008. How too much care kills species: Grassland reserves, agri-environmental schemes and extinction of Colias myrmidone (Lepidoptera: Pieridae) from its former stronghold. J. Insect Conserv. 12 (5), 519–525.
doi: 10.1007/s10841-007-9092-7

Latacz-Lohmann, U., Schilizzi, S., 2005. Auctions for conservation contracts: A review of the theoretical and empirical literature. Tech. rep., Report to the Scottish Executive Environment and Rural Affairs Department.
`http://www.scotland.gov.uk/Publications/2006/02/21152441/0`

Latacz-Lohmann, U., Van der Hamsvoort, C. P. C. M., 1998. Auctions as a means of creating a market for public goods from agriculture. J. Agr. Econ. 49 (3), 334–345.

Levins, R., 1969. Some demographic and genetic consequences of environmental heterogenity for biological control. Bull. Entomol. Soc. Am. 15, 237–240.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D. A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294 (5543), 804–808. doi: 10.1126/science.1064088

MA, 2005. Millenium Ecosystem Assesment: Ecosystems and Human Well-being: Biodiversity Synthesis. Tech. rep., World Resources Institute, Washington, DC.

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., Bazzaz, F. A., 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications 10 (3), 689–710.

Margules, C. R., Pressey, R. L., 2000. Systematic conservation planning. Nature 405 (6783), 243–253.
doi: 10.1038/35012251

McCann, K. S., 2000. The diversity-stability debate. Nature 405 (6783), 228–233.
doi: 10.1038/35012234

Nicholson, E., Possingham, H. P., 2006. Objectives for multiple-species conservation planning. Conserv. Biol. 20 (3), 871–881.
doi: 10.1111/j.1523-1739.2006.00369.x

Nordhaus, W. D., 2007. The Stern Review on the Economics of Climate Change. NBER Working Paper No. W12741.
`http://ssrn.com/abstract=948654`

Ovaskainen, O., Hanski, I., 2003. Extinction threshold in metapopulation models. Ann. Zool. Fenn. 40 (2), 81–97.

Panayotou, T., 1994. Conservation of biodiversity and economic development: The concept of transferable development rights. Environ. Resour. Econ. 4 (1), 91–110.
doi: 10.1007/BF00691934

Polasky, S., 2008. Why conservation planning needs socioeconomic data. Proc. Natl. Acad. Sci. U. S. A. 105 (18), 6505–6506.
doi: 10.1073/pnas.0802815105

Polasky, S., Nelson, E., Lonsdorf, E., Fackler, P., Starfield, A., 2005. Conserving species in a working landscape: land use with biological and economic-objectives (vol 15, pg 1387, 2005). Ecol. Appl. 15 (6), 2209–2209.

Pressey, R. L., Cabeza, M., Watts, M. E., Cowling, R. M., Wilson, K. A., 2007. Conservation planning in a changing world. Trends in Ecology & Evolution 22 (11), 583–592.
doi: 10.1016/j.tree.2007.10.001

Rabl, A., 1996. Discounting of long-term costs: What would future generations prefer us to do? Ecol. Econ. 17 (3), 137–145.
doi: 10.1016/S0921-8009(96)80002-4

Salzman, J., 2005. Creating markets for ecosystem services: Notes from the field. New York U. Law Rev. 80 (3), 870–961.

Salzman, J., Ruhl, J. B., 2000. Currencies and the commodification of environmental law. Stanford Law Rev. 53 (3), 607–694.

Saunders, D. A., Hobbs, R. J., Margules, C. R., 1991. Biological consequences of ecosystem fragmentation: A review. Conserv. Biol. 5 (1), 18–32.
doi: 10.1111/j.1523-1739.1991.tb00384.x

Simberloff, D., 1998. Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? Biological Conservation 83 (3), 247–257.

Stern, N., S.Peters, V.Bakhshi, A.Bowen, C.Cameron, S.Catovsky, D.Crane, S.Cruickshank, S.Dietz, N.Edmonson, S.-L.Garbett, L.Hamid, G.Hoffman, D.Ingram, B.Jones, N.Patmore, H.Radcliffe, R.Sathiyarajah, M.Stock, C.Taylor, T.Vernon, H.Wanjie, D.Zenghelis, 2006. Stern Review: The Economics of Climate Change. Tech. rep., HM Treasury.

Tietenberg, T., 2006. Emissions Trading Principles and Practice, 2nd Edition. RFF Press.

Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. Ecology 75 (1), 2–16, highcite.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W. H., Simberloff, D., Swackhamer, D., 2001. Forecasting Agriculturally Driven Global Environmental Change. Science 292 (5515), 281–284.
doi: 10.1126/science.1057544

UNEP, 1992. Convention on biological diversity. Tech. rep., UNEP, accessed 1.12.2009.
`http://www.cbd.int/doc/legal/cbd-un-en.pdf`

Weitzman, M. L., 1974. Prices vs quantities. Rev. Econ. Stud. 41 (128), 477–491.

Weitzman, M. L., 1998. Why the far-distant future should be discounted at its lowest possible rate. J. Environ. Econ. Manage. 36 (3), 201–208.
doi: 10.1006/jeem.1998.1052

Wiens, J. A., Stenseth, N. C., Vanhorne, B., Ims, R. A., 1993. Ecological mechanisms and landscape ecology. Oikos 66 (3), 369–380.

Wilcove, D. S., Lee, J., 2004. Using economic and regulatory incentives to restore endangered species: Lessons learned from three new programs. Conserv. Biol. 18 (3), 639–645.

Wissel, S., Wätzold, F., 2008. Applying tradable permits to biodiversity conservation: A conceptual analysis of trading rules. UFZ Discussion Paper 7/2008.

Wünscher, T., Engel, S., Wunder, S., 2008. Spatial targeting of payments for environmental services: A tool for boosting conservation benefits. Ecological Economics 65 (4), 822–833.
doi: 10.1016/j.ecolecon.2007.11.014

Wätzold, F., Drechsler, M., 2005. Spatially uniform versus spatially heterogeneous compensation payments for biodiversity-enhancing land-use measures. Environmental & Resource Economics 31 (1), 73–93.
doi: 10.1007/s10640-004-6979-6

Wätzold, F., Schwerdtner, K., 2005. Why be wasteful when preserving a valuable resource? A review article on the cost-effectiveness of European biodiversity conservation policy. Biol. Conserv. 123 (3), 327–338.
doi: 10.1016/j.biocon.2004.12.001

Wu, J. J., Babcock, B. A., 1996. Contract design for the purchase of environmental goods from agriculture. Am. J. Agric. Econ. 78 (4), 935–945.
doi: 10.2307/1243850

Wunder, S., 2007. The efficiency of payments for environmental services in tropical conservation. Conserv. Biol. 21 (1), 48–58.
doi: 10.1111/j.1523-1739.2006.00559.x

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