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Effects of space-dependent ecological benefits
and cost heterogeneity on habitat allocation**

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Abstract

This paper is concerned with the cost-effective allocation of habitat for endangered species under spatio-temporally heterogeneous economic development. To address the dynamic dimension of the problem we consider tradable development rights (TDR) as the instrument of choice. A particular challenge in applying TDR is that the ecological benefit of an individual habitat patch depends on its spatial relationship with other habitats and thus is an emergent rather than a fixed property. We analyse the spatial and temporal dynamics of habitats in a region under a TDR market that takes spatial interaction of habitats explicitly into account. We show that depending on the levels of spatial interaction and cost heterogeneity, two different outcomes may emerge: an “ordered” structure where habitats are clustered in space and stable over time, and a “disordered” structure where habitats are scattered in space and subject to high turnover of destruction and recreation.

1. Introduction

This paper is concerned with the problem that a conservation agency wishes to designate a certain proportion of an area as reserves in a cost-effective manner (i.e. that a given ecological target is achieved at lowest costs) in a dynamic setting. At least in principle, the agency is able to select the cost-effective spatial allocation of habitats in a static setting (cf. Ando et al., 1998; Polasky et al., 2001). In a dynamic perspective, however, changing land prices may lead to a situation where the initially cost-effective selection is not cost-effective anymore. In order to re-establish a cost-effective allocation, the agency would be confronted with the problem of designating new areas as reserves and allowing in former reserves economic development. Such a bureaucratic approach requires a high level of information on the side of the agency and is also very sensitive to political lobbying activities regarding the questions which areas shall be released for economic development and which areas shall be designated reserves.

An alternative to this bureaucratic approach to addressing changing land prices are tradable development rights. Based on the concept of tradable permits, such a system would allow economic development of a formerly conservation area if a permit is submitted to the conservation agency which certifies that an area with no conservation value has been transformed back into a conservation area of ecological value equal to the area to be destroyed. There is no requirement that developers establish new habitats themselves, but the permit can be bought from other landowners. This allows a market for tradable development rights to emerge.

The instrument of tradable permits has gained increasing popularity in environmental policy. It has been applied in a wide range of fields in air pollution control (see Tietenberg (2006) for an overview) and is moving increasingly into other areas with the EU CO₂-emissions trading scheme being the most prominent example of a recent application (e.g., Hansjürgens, 2005). However, until now there are only a few schemes related to biodiversity conservation that exhibit at least some elements of trading. One example is species conservation banking in the United States. A conservation bank is a piece of private land that is conserved and managed in perpetuity under a conservation easement to protect rare species. The party that holds the easement is granted credits by a federal or state agency for the land's conservation value. These credits may be used to address a bank owner's mitigation required by law. However, it may also be sold to other landowners with mitigation requirements (Fox and Nino-Murcia, 2005). Another example of conservation related trading opportunities exists in Brazil where regulations require each rural property to maintain a proportion of forest under natural vegetation. Recent provisional regulations allow landowners to satisfy the requirement for one property through a forest reserve located on another. The reserve site may be owned by another party, opening the possibility of trading land development rights (Chomitz et al., 2004).

One of the challenges of applying tradable permits to biodiversity conservation arises because the ecological value of habitats for the survival of species is space dependent, i.e. it depends on the presence and location of other habitats (e.g. Hanski, 1999; Ovaskainen and Hanski, 2003). The purpose of this paper is to analyse, using a conceptual model, how these spatial interdependencies influence the allocation of habitat areas and areas for economic development over time, if a market for tradable development rights exists.

The model considers a setting with stochastic changes in the opportunity costs, and the flexibility of the market for development rights is used to adapt to this change. We will show

how the space-dependence of the ecological benefit and the dynamics in the opportunity costs affect the dynamics in the market for tradable development rights and, particularly, the spatio-temporal dynamics of the habitat network in the landscape. The next Section presents the model, which is solved partly analytically and partly numerically in Section Three. The results are discussed in the final Section.

2. The model

Consider a landscape with $N \gg 1$ areas, numbered $i=1 \dots N$, of (without loss of generality) identical sizes. Whether an area can serve as a habitat depends on the type of use. Land may be either used for economic purposes and is of no conservational value, or it may be used for conservation which leads to opportunity costs in terms of foregone economic development. Let $\mathbf{x}$ be a vector with N elements that can take values of 1 and 0, where $x_i=1$ indicates that area i is a habitat and $x_i=0$ otherwise. Let $\mathbf{r}=(\mathbf{r}_1, \dots, \mathbf{r}_N)$ be an N -element vector containing the spatial co-ordinates $\mathbf{r}_i=(x_i, y_i)$ of the areas $i=1 \dots N$. Let $V(\mathbf{x}, \mathbf{r})$ be the ecological benefit of the landscape structure defined by $\mathbf{x}$ and $\mathbf{r}$. Assume the ecological benefit is separable, i.e. can be written as the sum of local benefits¹ $v_i(\mathbf{x})$:

$$V(\mathbf{x}, \mathbf{r}) = \sum_i x_i v_i(\mathbf{x}, \mathbf{r}) \quad (1)$$

The local benefit that is realised if area i is turned into and/or maintained as habitat ($x_i=1$) then can be broken down into

$$v_i(\mathbf{x}, \mathbf{r}) = \varepsilon + \mu_i(\mathbf{x}, \mathbf{r}) \quad (2)$$

where

$$\varepsilon = \varepsilon_i = \lim_{\substack{|\mathbf{r}_i - \mathbf{r}_j| \rightarrow \infty \\ \forall j \neq i}} V(x_1, \dots, x_{i-1}, 1, x_{i+1}, \dots, x_N, \mathbf{r}) - V(x_1, \dots, x_{i-1}, 0, x_{i+1}, \dots, x_N, \mathbf{r}) \quad \forall i = 1 \dots N \quad (3)$$

is the benefit of adding an isolated habitat i (infinitely far away from all other habitats), termed the habitat's "self benefit" and identical for all areas i , and

$$\mu_i(\mathbf{x}, \mathbf{r}) = V(x_1, \dots, x_{i-1}, 1, x_{i+1}, \dots, x_N, \mathbf{r}) - \lim_{\substack{|\mathbf{r}_i - \mathbf{r}_j| \rightarrow \infty \\ \forall j \neq i}} V(x_1, \dots, x_{i-1}, 1, x_{i+1}, \dots, x_N, \mathbf{r}) \quad (4)$$

is the "location benefit", i.e. the increase in the benefit of habitat i if this is shifted from an isolated position ($|\mathbf{r}_i - \mathbf{r}_j| \rightarrow \infty, \forall j \in J = \{j \neq i \mid x_j = 1\}$) to another position $\mathbf{r}_i$. In contrast to the self benefit, the location benefit is a result of the interaction among habitats and depends on the landscape structure $\{\mathbf{x}, \mathbf{r}\}$ (including the location of area i itself, $\mathbf{r}_i$).

Regarding the initial allocation of development rights we assume that the regulator sets a target value Y for the ecological benefit $V(\mathbf{x}, \mathbf{r})$ of the whole area and requires each land owner to contribute an (average) target value $y=Y/N$. The owner of area i ($i=1 \dots N$) can now decide to create and/or maintain her or his area as habitat ($x_i=1$) and earn a certificate of value $z_i=v_i-y$ which may be offered on the market at a price p . Alternatively, the owner may not wish to have a habitat on her or his area ($x_i=0$). To fulfil the rules of the scheme in this case, the

¹ Note that this assumption does not imply any assumption of linearity. The non-linear function $V=\prod_i v_i$, e.g., can be transformed into $V'=\ln(V)=\sum_i \ln(v_i)$ and V' considered instead of V . Therefore the loss of generality here is less severe than it might look like on first sight.

owner has to buy a certificate of value y at price p on the market. With the cost of creating and maintaining area i as habitat denoted as c_i , the choice between these two options is made with the aim of maximising the profit

$$\pi_i(x_i) = -c_i x_i + p[v_i(\mathbf{x}, \mathbf{r})x_i - y] \quad (5)$$

Whether $x_i=1$ or 0 maximises π_i depends on the market price of certificates, p :

$$x_i(p) = \begin{cases} 1 & p > v_i / c_i \\ 0 & \text{otherwise} \end{cases} \quad (6)$$

The value of the certificate bought or sold by the owner of area i is

$$z_i = x_i v_i(\mathbf{x}, \mathbf{r}) - y \quad (7)$$

where a positive (negative) value represents a situation where the owner is a seller (buyer). The market price p is given by an equality of supply and demand of certificates:

$$\sum_i z_i = \sum_i (x_i(p) v_i(\mathbf{x}, \mathbf{r}) - y) = 0 \quad (8)$$

Due to eq. (5) this immediately leads to fulfilment of the regulator's objective

$$V(\mathbf{x}, \mathbf{r}) = Y \quad (9)$$

We now put this model into a dynamic setting by introducing economic dynamics in the region that is expressed by temporal variation of the costs c_i . To model the temporal dynamics of the c_i in the simplest way, we consider discrete time periods and assume that in each time period the costs c_i are sampled randomly and independently from a uniform distribution with mean $\bar{c}$ and width 2σ :

$$f(c) = \begin{cases} (2\sigma)^{-1} & |c - \bar{c}| \leq \sigma \\ 0 & \text{otherwise} \end{cases} \quad (10)$$

Within the scope of the model analysis, the assumption of a constant mean $\bar{c}$ does not impose a loss of generality, as will be shown below.

Finally, we introduce three aggregated variables that will be of interest: the total number of habitat areas,

$$A = \sum_{i=1}^N x_i, \quad (11)$$

the cost over all areas

$$C = \sum_{i=1}^N x_i c_i \quad (12)$$

(which due to eq. (8) is equal to minus the sum over all profits π_i), and the total location benefit

$$M = \sum_{i=1}^N x_i \mu_i(\mathbf{x}, \mathbf{r}) \quad (13)$$

Location benefit and area are inversely related due to

$$Y = V = \sum_{i=1}^N v_i = \varepsilon \sum_{i=1}^N x_i + \sum_{i=1}^N x_i \mu_i(\mathbf{x}, \mathbf{r}) = \varepsilon A + M \quad (14)$$

3. Model analysis

Below the model will be investigated partly analytically and partly numerically. The focus will be on the long-term behaviour of the model. To prepare the mathematical calculations we rescale the model parameters to dimensionless quantities in order to eliminate redundant parameters and simplify the analysis. We scale costs c_i and their range σ as well as the profits π_i and the total costs C in units of $\bar{c}$, the location benefit $\mu(\mathbf{x}, \mathbf{r})$, the total location benefit M and the benefit target Y in units of ε , and the price p in units of $\bar{c} / \varepsilon$ to obtain

$$\begin{aligned} c_i' &= \frac{c_i}{\bar{c}}, \quad \sigma' = \frac{\sigma}{\bar{c}}, \quad \pi_i' = \frac{\pi_i}{\bar{c}}, \quad C' = \frac{C}{\bar{c}}, \\ \mu_i'(x, r) &= \frac{\mu(x, r)}{\varepsilon}, \quad Y' = \frac{Y}{\varepsilon}, \quad y' = \frac{y}{\varepsilon}, \quad M' = \frac{M}{\varepsilon}, \quad p' = \frac{p\varepsilon}{\bar{c}} \end{aligned} \quad (15)$$

The model equations then become

$$\pi_i(x_i) = -x_i c_i' + p[(1 + \mu_i'(\mathbf{x}, \mathbf{r}))x_i - y'] \quad (5')$$

and

$$f(c')dc' = \begin{cases} (2\sigma')^{-1}dc' & |c - \bar{c}| \leq 1 \\ 0 & \text{otherwise} \end{cases} \quad (10')$$

To simplify the notation we drop the primes again and continue the analysis with the dimensionless parameters. As can be seen, the mean cost $\bar{c}$ does not occur any more in the model equations which shows that temporal changes in $\bar{c}$ affect the model dynamics only in a trivial way in a sense that ceteris paribus all economic quantities like prices and costs change with $\bar{c}$ in a proportional manner.

3.1 Analytical results

Some of the model dynamics can be deduced analytically under three assumptions regarding the spatial properties of the benefit function V .

1. The location benefit of an area i decreases with increasing distance to other areas containing habitat: $d\mu_i(\mathbf{x}, \mathbf{r})/d|\mathbf{r}_j - \mathbf{r}_i| < 0$ for all $j \in J = \{j \neq i \mid x_j = 1\}$. This means that habitats close together lead to a higher location benefit than habitats far apart.
2. The location benefit is negligible if the distance to any other area j that contains habitat exceeds a certain threshold ρ , i.e. if $|\mathbf{r}_i - \mathbf{r}_j| \geq \rho$ for all $j \in J = \{j \neq i \mid x_j = 1\}$. This means that the interaction between habitats defined in (1) has a limited range, ρ .
3. If all areas contain habitat ($x_i=1$, all $i=1 \dots N$) the location benefit $\mu_i(\mathbf{x}, \mathbf{r})$ is approximately independent of i and given by $\mu_i(\mathbf{x}, \mathbf{r})=m$. This is achieved if either $\mu_i(\mathbf{x}, \mathbf{r})$ is independent of the location of areas within radius ρ for all i , or ρ is large enough such that the distribution of the pair-wise differences between areas within the circle spanned by ρ is independent of i . The quantity m may be interpreted as the maximum possible location benefit in the landscape.²

To illustrate the meaning of these assumptions consider the example where all areas $i=1 \dots N$ are located on a regular square grid with inter-area distance d . The location benefit of an area i may be obtained by counting the number of areas adjacent to area i that contain habitat:

$$\mu_i(\mathbf{x}, \mathbf{r}) = w \sum_{j \in J_d} x_j \text{ with } J_d = \{j \neq i \mid |\mathbf{r}_j - \mathbf{r}_i| < 2d\} \quad (16)$$

where w is some positive constant that measures how much the location benefit contributes to the total benefit compared to the self benefit (cf. eq. 2). By this setting the location benefit would range between zero (if area i is completely isolated) and $8w$ for an area that is completely surrounded by habitats. Equation (15) represents a next-neighbour interaction between habitats that is extremely short-ranged. Habitats with distance to area i that is greater or equal to $\rho=2$ do not contribute to $\mu_i(\mathbf{x}, \mathbf{r})$. Within the radius ρ each habitat contributes an amount w to $\mu_i(\mathbf{x}, \mathbf{r})$ regardless of its precise location. Consequently, in the case of all areas in the landscape containing habitat ($x_i=1$), $\mu_i(\mathbf{x}, \mathbf{r})=8w=m$ for all i , which fulfils condition (3).

Under these assumptions, consider the special case of zero variation in the costs: $\sigma=0$. Here the total cost becomes

$$C = A = \sum_{i=1}^N x_i \quad (17)$$

and

$$Y = C + M \quad (18)$$

As the land-owners attempt to maximise their profits, they attempt to minimise C which is achieved by maximising M (note that all areas have the same cost, as $\sigma=0$). Due to assumption 1, M is maximised by clustering all areas that contain habitats. If these habitat clusters are sufficiently large compared to the range of $\mu_i(\mathbf{x}, \mathbf{r})$ (assumption 2) we can ignore boundary effects, such that there are only two types of areas in the landscape:

- (1) Habitat areas ($x_i=1$): they belong to a habitat cluster and therefore have location benefit $\mu_i(\mathbf{x}, \mathbf{r})=m$ (assumption 3)

² Condition 3 is always fulfilled if the areas are arranged on regular (e.g. square or hexagonal) grids.

- (2) Non-habitat areas ($x_i=0$): they belong to a cluster that contains only non-habitat and therefore have location benefit $\mu_i(\mathbf{x}, \mathbf{r})=0$.

With this eq. (12) simplifies to

$$M_0 \equiv M(\sigma = 0) = m \sum_{i=1}^N x_i \quad (19)$$

and with eqs. (16) and (17) we obtain for the total cost

$$C_0 \equiv C(\sigma = 0) = \frac{Y}{1+m} \quad (20)$$

We measure the benefit target y against its possible maximum $y_{\max}=1+m$ and define

$$\lambda = \frac{y}{y_{\max}} \quad \text{with} \quad y_{\max} = 1+m$$

The total cost and total area then becomes

$$C_0 = A_0 = N\lambda \quad (21)$$

and the total location benefit

$$M_0 = mC_0 = Nm\lambda \quad (22)$$

Now gradually increase σ . As long as the clusters remain stable and are sufficiently large ($N, Y \gg 1$), we can assume that the probability that an area i has cost c_i is relatively independent of whether the area contains habitat ($x_i=1$) or not. The distribution of the c_i , in particular the mean cost, then is the same in all clusters and equal to the mean cost in the entire landscape (which equals 1 after the above rescaling operations).

A habitat cluster which contains certificate suppliers becomes unstable as soon as suppliers switch to become buyers. As μ is identical for all suppliers, the first suppliers to switch are those with the highest cost (eqs. (5), (6)), i.e. those that have cost $c_i=1+\sigma$. The certificate price p where these land-owners are indifferent between supplying and buying is given by $p_s=(1+m)/(1+\sigma)$ (eq. 6). Analogously, a non-habitat cluster containing buyers becomes unstable if buyers switch to become suppliers. The first buyers to switch are those with minimal costs ($c_i=1-\sigma$) which are indifferent between buying and supplying if the price is $p_b=1-\sigma$.

If $\sigma < \sigma_c$ with

$$\sigma_c = \frac{m}{2+m} \quad (23)$$

we find $p_s < p_b$ and there is a range of market prices $p_s < p^* < p_b$ where the equilibrium of demand and supply leads to stable clusters and where total cost and total location benefit are given by eqs. (20) and (21). At the critical point $\sigma = \sigma_c$ the feasible interval $p_s < p^* < p_b$ contracts to a single unique market price

$$p_c = \frac{2}{2+m} \quad (24)$$

For $\sigma > \sigma_c$ some buyers and sellers will switch their behaviour, meaning that some habitat area in a habitat cluster is developed and some non-habitat in a non-habitat cluster is retransformed into habitat. As a consequence, the formerly clear boundaries between the clusters start to dissolve.

To conclude, for $\sigma < \sigma_c$ the ecological-economic system is in an “ordered phase”³ with stable clusters and total cost, area and location benefit given by eqs. (21) and (22). For larger σ we observe a disordered phase. The critical cost variation σ_c increases with the maximum location benefit m . For $m \ll 1$ we have $\sigma_c \approx m$; for larger m , σ_c asymptotically approaches a value of 1. For $m \ll 1$ the critical price is $p_c \approx 1$; for larger m it decreases with increasing m and asymptotically approaches a value of 0.

3.2 Numerical analysis

As the analytical investigation of the disordered phase, $\sigma > \sigma_c$, is very demanding and would be beyond the scope of the present paper, we employ numerical simulation on the basis of a specific location benefit function. We choose the next-neighbour function introduced above

$$\mu_i(\mathbf{x}, \mathbf{r}) = w \sum_{j \in J_d} x_j \text{ with } J_d = \{j \neq i \mid |\mathbf{r}_j - \mathbf{r}_i| < 2d\} \quad (16)$$

We assume the areas are located on a regular square grid with cyclical boundaries. The dimension of the grid is 50x50 unless stated otherwise. The maximum location benefit here is $m=8w$ and the maximum local benefit is $y_{\max}=1+8w$. For each area we draw the costs c_i from a random distribution according to eq. (10). The initial distribution of habitat $\mathbf{x}$ in the landscape is chosen randomly; it plays no role for the long-term behaviour of the model as long as there is at least one area with $x_i=0$ and one area with $x_i=1$. From the x_i we determine the local benefits, v_i which together with the c_i form the inputs for the habitat trade. To determine the equilibrium permit price p^* (cf. eq. 8) we scan the range of mathematically feasible prices until p^* has been found. Knowing for each area if it remains habitat/non-habitat or switches its state, we update the x_i and enter the next time period. In this and all following time periods we proceed as in the initial period, i.e. we start by randomly drawing the costs c_i and end with the determination of the market equilibrium.

We are interested in the long-term behaviour of the model where price p^* , total cost C and total location benefit M are stationary. To determine the stationary values we simulate for 1000 periods to reach the stationary state and then for another 200 periods to calculate a

³ This behaviour is similar to that of various physical systems that undergo a so-called phase transition when the temperature crosses a critical level (e.g., Landau and Lifshitz 1969). Consider, e.g., a ferromagnet. If the temperature is below a critical level, so-called clusters form in which all spins (“elementary magnets”) point in the same direction. One speaks of an ordered phase. If the temperature is increased beyond the critical level, the high thermal energy destroys the magnetic order, the clusters disappear and the directions of the spins become random. One speaks of a disordered phase.

temporal average of the variables of interest which are the equilibrium price p and the total area A and cost C .

Figure 1 shows the development of the habitat pattern for two different levels of cost variation σ . For $\sigma=0.55 < \sigma_c=0.58$ an ordered phase with separated habitat and non-habitat clusters is reached relatively quickly whereas for $\sigma=0.6 > \sigma_c$ no order can be observed, even after long simulation time.

Disorder means a reduced location benefit which due to eq. (14) means that total area must be larger to fulfil the benefit target Y . Figure 2 shows that at the critical level of cost variation σ_c total area sharply (note the scales of Fig. 2) jumps from close to A_0 (eq. 21) to a larger value. The larger the total number, N , of areas the steeper is the jump. We conclude that the sharp increase of A with σ indicates the transition σ_c between the ordered and the disordered phases. Figure 3 confirms for all possible combinations of model parameters w and σ that the market and the habitat network are either in an ordered (with small total area) or a disordered phase (with high total area) which are clearly separated from each other. Analogous results can be obtained for other values of conservation target λ . The numerical results of Fig. 3 very well agree with the theoretical calculations which are further confirmed by the analysis of the “critical” price p_c that is obtained at the critical point σ_c (Fig. 4).

So far we have considered the spatial aspects of the habitat dynamics. To complete the analysis we turn to the habitat dynamics created by the market. To quantify these dynamics we consider the “turnover rate” of habitats, i.e. the rate by which a habitat area turns into a non-habitat area or vice versa. We measure habitat turnover by the correlation coefficient

$$\eta(t) = \frac{4}{N} \sum_{i=1}^N [x_i(t) - 0.5] \times [x_i(t-1) - 0.5] \quad (24)$$

If there is no turnover in area i such that x_i remains constant between two consecutive periods t and $t+1$ then area i contributes an amount $1/N$ to the quantity η . If there is turnover, such that x_i changes from 0 to 1 or from 1 to 0 then area i contributes an amount $-1/N$ to η . The correlation coefficient therefore ranges from -1 where there is turnover in all N areas to $+1$ where there is no turnover at all. An alternative interpretation is: for $\eta = 1$ a given area switches its state x_i with probability 0, for $\eta = 0$ it switches with probability 0.5 and for $\eta = -1$ it switches with probability 1.

Figure 5 shows the correlation coefficient as a function of w and σ . In the ordered phase (cf. Fig. 3) habitat turnover is very small (η close to 1), i.e. the habitat structure is not only clumped but also stable in time. In the disordered phase, habitat turnover is almost exclusively triggered by the random fluctuations of the costs c_i and therefore the correlation of x_i between subsequent periods is close to $\eta=0$ (i.e. probability of switching states is 0.5).

Discussion

We have modelled a market for development rights in a landscape where areas can either be conserved as habitat or used for economic purposes (non-habitat). Land-owners trade rights to destroy habitat and use it for economic development. The opportunity costs of maintaining an area as habitat differ among areas and vary over time. Space plays an important role in that the ecological value of a habitat depends on its location; in particular, to what extent other habitats exist in its vicinity. Based on ecological theory (e.g., Hanski, 1999; Ovaskainen and Hanski, 2003), we assumed that the ecological value of a habitat increases when more habitats are found in its neighbourhood. In our model, this spatial interaction leads to self-organised habitat dynamics in the considered landscape.

Being interested in the stationary behaviour of the model, we found two possible phases the dynamics can be in: an ordered or a disordered phase. In the ordered phase the areas containing habitat are clustered in space, while in the disordered phase they are scattered. The ordered phase is obtained if the variation in the opportunity costs lies below a critical value that is determined by the spatial interaction between the ecological values of the habitats. If the value of a habitat very strongly depends on the presence of other habitats in its neighbourhood, more variation in the opportunity costs is allowed to keep the ordered phase. If the variation in the opportunity costs exceeds the critical value, the system runs into a disordered phase. In a way, the dynamics can be seen as a struggle between two forces: the interaction between the ecological values of the habitats is the ordering force that leads to a clustering of habitats; the random variation in the opportunity costs tends to tear habitat clusters apart and lead into disorder. The outcome of the dynamics is determined by the prevailing force.

The relevance of these results for conservation is both of an economic and an ecological nature. The analysis showed that in the disordered phase the conservation objective can be achieved at lower costs, because ecological benefit is not only achieved through mere quantity of habitat but also through “quality” of habitat arrangement. The ecological relevance lies in the fact that in the ordered phase there are fewer turnovers between habitat and non-habitat, because most habitats are surrounded by other habitats and thus have high ecological value. Even if by chance their opportunity costs become very high it will still be more profitable to maintain them as habitat (cf. the discussion of the critical point). Habitat destruction will take place only at the boundary of the habitat and non-habitat clusters, where habitats are less surrounded by others.

What is the ecological effect of habitat turnover? So far we have considered only habitats and their spatial configuration, but of course the regulators actual aim is to conserve the species on these habitats. Habitat turnover means that individuals are chased away or even killed where habitat is destroyed and even if at the same time another habitat is created this has to be colonised by individuals from other habitats, which requires sufficient time and dispersal ability of the species. In any case habitat turnover leads to a disruption of species dynamics and increases the extinction risk of most species (e.g., Gyllenberg and Hanski, 1997; Johst et al., 2002). Therefore, the disordered phase has an implicit ecological cost attached to it that needs to be considered explicitly in future studies.

The analysis contains a number of assumptions which are worth discussing. The first is that of the separability of the ecological benefit function (eq. 1). Although for most relevant ecological benefit functions it should be possible to approximate them by functions that via some monotonic transformation can be transformed into a separable function, there may be

situations where this is not possible. In this case one would have to restrict the market in a way that only a small fraction of habitats may be traded at one time. The local benefits v_i of each of these habitats then may be regarded as their marginal benefits $v_i = V(x_i=1) - V(x_i=0)$ and no restricting assumption on V is necessary any more.

Another important assumption is that the spatial range of interaction between the ecological values of habitats is short compared to the size of the habitat cluster. If the range of interaction is increased, the spatial boundary between habitat-clusters and non-habitat will become broader and the transition from the ordered to the disordered phases probably be smoother and set in earlier.

In our analysis we assumed that land price changes are independent of the land-use type of the surrounding areas. This is an assumption that may be modified. E.g. economic development is often spatially concentrated due to positive externalities (e.g. Henderson, 2003). This means that land prices close to an area with economic development are more likely to increase than land prices in other areas. Further research may consider feed-back loops that arise when land prices not only affect land-use change but also the opposite relationship exists.

A key assumption of this paper is that the value of a habitat depends on the number of habitats within some neighbourhood. This is a useful assumption for the purpose of this paper because it captures the effects of space-dependence on land allocation in the context of tradable development rights. However, when designing rules for tradable development schemes, the schemes' effectiveness might be improved by employing ecologically more realistic benefit functions that address the above mentioned issue of habitat turnover and more complex spatial interactions. Next to sophisticated analytical formulas (e.g., Frank and Wissel, 2002), simulation models (e.g. Johst et al., 2006) may be used to measure ecological benefit. Such assessments, however, mean more complicated trading rules and, hence, are likely to incur higher transaction costs. A challenge of future research, therefore, is the design of ecological benefit functions that are simple enough to be implemented and still provide a sufficiently good approximation of the true ecological benefit of a habitat.

The implementation of a scheme for tradable development rights where the value of a habitat depends on the land-use type of neighbouring areas may be difficult to implement in practice. The main reason is that it requires a re-evaluation once the land-use of adjacent areas changes. Re-evaluations are costly and they may be perceived as unfair, because they are not a result of the actions of the land-owners themselves but of other land-owners. They may also be unpopular with conservation groups because if an area is partly economically developed those land-owners who still keep their areas as habitats not only do not profit from transferring their land but additionally get 'punished' by having to acquire additional development rights. Furthermore, in some countries legal reasons of protection of confidence may prevent such a scheme. A scheme that takes these concerns into account, and where the ecological benefit of a habitat depends, e.g., only on its size, however, is naturally less cost-effective. Further research may address the extent of the loss in cost-effectiveness under various ecological benefit functions.

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Figure captions

Figure 1: Pattern of habitat (black) and non-habitat (white) areas after 10, 100, and 1000 simulation periods for $\sigma < \sigma_c = 0.58$ and for $\sigma > \sigma_c$ (other parameters $w=0.36$, $\lambda=0.5$).

Figure 2: Total area (scaled in units of A_0) as a function of cost variation σ for various numbers of area: $N=50^2$, 100^2 , 200^2 , 400^2 . Other parameters: $\lambda=0.5$ and $w=0.36$.

Figure 3: Total area A as a function of w and σ . The conservation target is set at $\lambda=0.5$. The line marks the set of critical points $(w, \sigma_c(w))$ after eq. (23) which separates the ordered and disordered phases.

Figure 4: Critical price $p_c = p(\sigma_c)$ as a function of the maximum location benefit m . Dotted line: from simulation; solid line: eq. (24).

Figure 5: Correlation coefficient of states x_i between two subsequent time periods. Similar to Fig. 2, the line separating the ordered phase with high correlation and the disordered phase with low correlation is given by eq. (23). The conservation target is $\lambda=0.5$.

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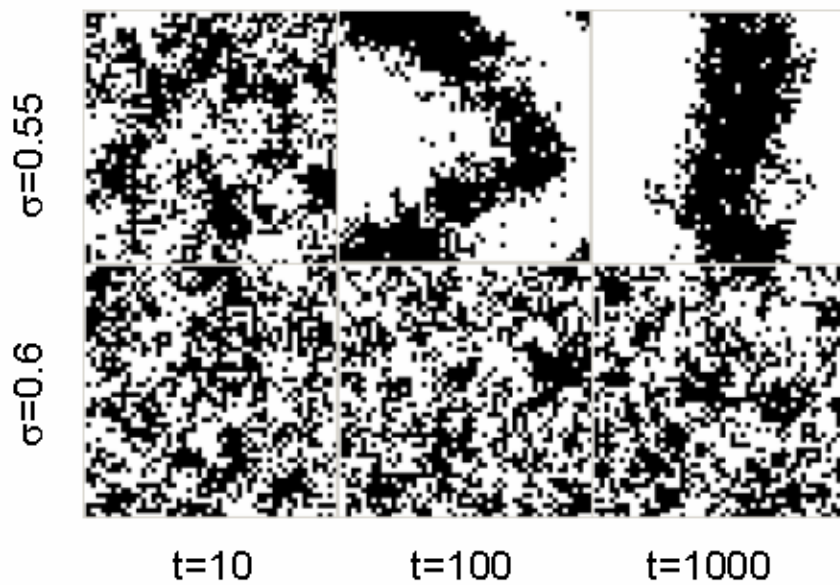


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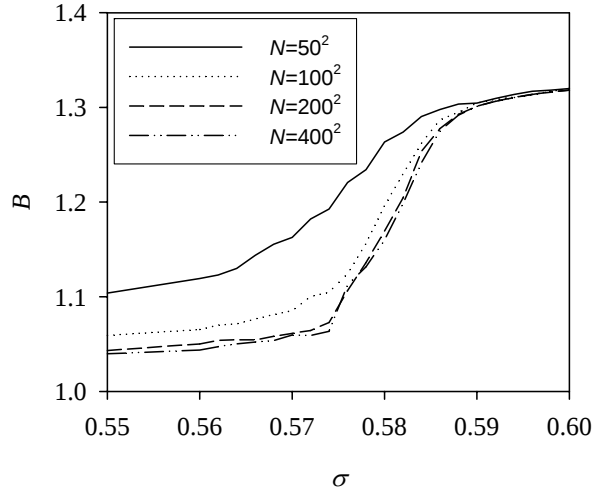


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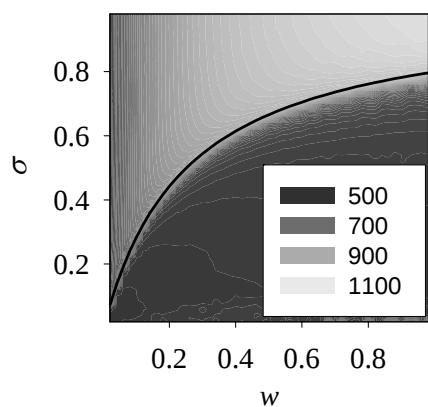


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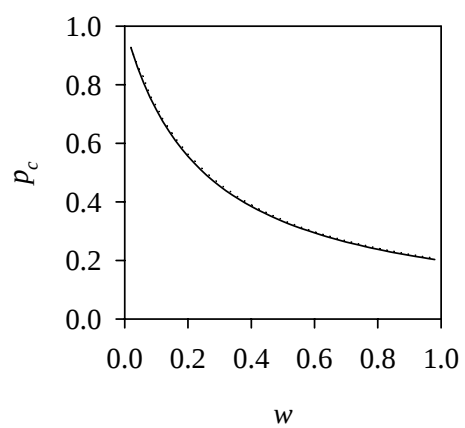


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