Spatially cost-effective species conservation in agricultural landscapes: an ecological-economic modeling synthesis

Rolf Groeneveld[1]
Wageningen University
Environmental Economics and Natural Resources Group
Hollandseweg 1
6709 PG Wageningen
The Netherlands
Telephone +31 317 485367
Fax +31 317 484933
http://www.sls.wageningen-ur.nl/enr
rolf.groeneveld@wur.nl

Abstract

This paper presents a spatially explicit analysis of cost-effective nature conservation strategies in agricultural areas. Because the spatial pattern of conservation measures is important for the ecological benefits of conservation, and also determines the costs of conservation, cost-effectiveness analysis of species conservation in agricultural areas needs to include a spatial dimension. Furthermore, because the relation between spatial habitat configuration and population size of the target species is likely subject to nonlinearities such as multiple equilibria and multiple optima, tools are needed that can take these effects in consideration.

This paper analyzes spatially cost-effective configuration of habitat areas under different assumptions with respect to transport costs and spatial configuration of potential habitat patches. A spatially explicit bioeconomic model is presented, consisting of a straightforward economic land use model as well as the Incidence Function Model (IFM) (Hanski, 1994).

The paper concludes that depending on the spatial configuration of candidate sites, multiple equilibria and optima in metapopulation dynamics are likely to cause nonconvexities in the production possibilities set of agricultural profits and species conservation. Furthermore, it is possible that conservation policy becomes locked in a suboptimal spatial strategy if it is initially designed under a smaller budget than is available in a later stage.

Keywords: land use, species conservation, incidence function model
JEL categories: Q15, Q24

---

[1] The author acknowledges useful comments on this paper by Ekko van Ierland and Hans-Peter Weikard. As usual, remaining errors are the sole responsibility of the author.

1 Introduction

Large numbers of known species in Western-Europe are threatened with local or global extinction (Delbaere, 1998). In the Netherlands, for example, 25 of the 64 known mammal species have either gone locally extinct or are threatened with local extinction; the same holds for 57 of 172 bird species and 499 of 1490 higher plant species, and for many other species groups similar figures can be found (RIVM/CBS/WUR, 2003). Generally speaking, general species are becoming more general, whereas rare species are becoming more rare (Bink *et al.*, 1994).

Land use changes have contributed seriously to biodiversity loss through habitat loss and habitat fragmentation. Many habitat disappeared when heath- and peatlands were converted to agricultural land, and land re-allotments caused the disappearance of many landscape elements such as hedgerows and small ditches. Lastly, infrastructure development fragmented the landscape even further (van Zanden and Verstegen, 1993; Bink *et al.*, 1994).

Habitat fragmentation has two effects on local populations: (i) reduced population size; and (ii) reduced interpatch dispersal. Local populations can go extinct by environmental disturbances and disasters, such as floods or extreme drought, but also by pure demographic coincidence, for instance low birth rates. As long as dispersal is frequent, these local extinctions may be prevented or ‘reversed’ by immigration from other local populations. Therefore, as local habitats become smaller, local populations are more likely to go extinct, and as they become more isolated, ‘vacated’ patches are less likely to be recolonized (see e.g. MacArthur and Wilson, 1967; Opdam *et al.*, 1993; Hanski and Gilpin, 1997).

As many of the direct causes of biodiversity decline have a clear economic rationale, halting or reversing biodiversity decline may be costly. In agricultural landscapes, measures to conserve species populations will be largely at the expense of agricultural activities. It is therefore important to develop cost-effective nature conservation strategies, i.e. strategies that achieve one objective (say, species conservation) without unnecessary losses to others (say, agricultural profits). Furthermore, many cost-effective strategies are possible depending on the desired level of species conservation. To develop efficient species conservation strategies, i.e. strategies that maximize net social welfare, insight is needed in the trade-off between agricultural profits and the target species population. Furthermore, as conservation of one species could take place at the expense of others, interspecies trade-offs also need to be addressed.

Ecological processes can have complex dynamics, and population dynamics are no exception (Hanski *et al.*, 1995; Holling *et al.*, 1995; Scheffer *et al.*, 2001). Empirical as well as theoretical analysis suggests that spatially dispersed populations might have alternative equilibria (Hanski *et al.*, 1995). Moreover, as restoration of habitat connectivity is one of the primary goals of species conservation in fragmented landscapes, it is likely that the trade-off between agriculture and species conservation has multiple optima, each optimum referring to a local cluster of habitat patches.

These complexities can have serious economic implications and should therefore be considered in cost-effectiveness analysis of spatial conservation strategies.

This paper presents a spatially explicit bioeconomic model to analyze the trade-off between species conservation and agricultural profits in a spatially explicit setting, including some of the nonlinearities that might occur in metapopulation dynamics. The model allocates land use types over a number of plots or patches, in order to maximize one of the objectives analyzed under the restriction that the other objectives do not drop below a prespecified threshold.

I use the incidence function model (IFM) (Hanski, 1994) to relate spatial land use allocation to the ecological objective. The IFM has four advantages that are particularly interesting for applied analysis in general, and for economic cost-effectiveness analysis in particular. First, the IFM has been applied in many theoretical and empirical ecological analyses and is well accepted by ecologists as a valuable tool to assess the ecological consequences of changing the spatial configuration of habitat patches (ter Braak *et al.*, 1998). Second, it includes the basic mechanisms in metapopulations, namely extinction and colonization, and is capable of capturing some of the nonlinearities that can be expected in metapopulation dynamics, namely multiple equilibria and multiple optima. Third, it is relatively straightforward as it contains few variables, which all have an unambiguous interpretation. Fourth, it can be estimated by means of field data that are relatively easy to collect.

The integrated IFM-land use model is used to demonstrate how multiple equilibria and optima in metapopulation dynamics might affect the trade-off between species conservation and agricultural profits, and between species with conflicting habitat requirements. These trade-offs are depicted by production possibilities frontiers of (i) agricultural profits and the expected number of habitat patches inhabited by a target species; and (ii) the expected number of habitat patches of two species with conflicting habitat requirements, under different assumptions regarding spatial configuration of candidate sites and transport costs.

Spatially explicit trade-off analyses of biodiversity and other land uses are mainly found in the forestry economics literature. The ecological objectives chosen in these studies vary from habitat characteristics or habitat area as indicators of ecological objectives (e.g. Rohweder *et al.*, 2000), to more explicit ecological objectives such as expected number of individuals (e.g. Hof and Raphael, 1997), relative abundance of several species (e.g. Conrad and Salas, 1993), or population viability (e.g. Calkin *et al.*, 2002). The ecological relations are mostly described by either an elaborate simulation model run for a large number of trials (e.g. Conrad and Salas, 1993) or by a simplified ecological model integrated in a general framework (e.g. Calkin *et al.*, 2002; Hof and Raphael, 1997).

Another branch of literature comprises the selection of a finite set of reserve sites from a larger set of candidate sites in order to maximize the number of species covered under a budget restriction or to conserve a fixed number of species at minimal costs. Generally dubbed the Reserve Site Selection Problem (e.g. Margules and Nicholls, 1988), the analysis has been extended to include financial restrictions and land prices (e.g. Polasky *et al.*, 2001), incomplete information (e.g. Polasky *et al.*, 2000), risk and uncertainty (Weikard, 2003), connectivity between reserves (e.g. Briers, 2002) and time (e.g. Costello and Polasky, 2002). Moilanen and Cabeza (2002) apply the IFM in reserve site selection for single species conservation, and this has so far been the only application of the IFM in optimization of spatial conservation strategies. It does not, however, explicitly include economic considerations.

The novel contribution of this analysis is threefold. First, instead of the simulation models and simplified ecological models used in previous economic analyses, this analysis uses a spatially explicit ecological model that is firmly rooted in metapopulation theory and is generally accepted by ecologists. Second, the analysis addresses complexities in metapopulation dynamics, more precisely multiple equilibria and optima, that have so far been neglected in spatially explicit economic trade-off analyses of species conservation and alternative land uses, and analyzes their effect on the production possibilities frontier. Third, the analysis includes interspecies trade-offs as well as the classical trade-off between species conservation and alternative land use.

The paper proceeds as follows. Section 2 explains the occurrence of multiple equilibria and multiple optima in metapopulation dynamics in more detail, and discusses their possible implications for cost-effective species conservation. Section 3 presents the mathematical structure of the model used to calculate production possibilities frontiers of species conservation and alternative land uses. Section 4 demonstrates the effects of multiple equilibria and optima on the production possibilities frontiers of species conservation and alternative land uses under different assumptions regarding spatial configuration of candidate sites and transport costs. Section 5 concludes.

2 Nonlinearities in spatial population dynamics and their possible implications for cost-effective species conservation strategies

Like many ecosystem processes, metapopulation dynamics can be strongly nonlinear processes. Theory suggests that metapopulations can have multiple point equilibria, limit cycles, or more complex attractors (Hanski and Gyllenberg, 1993; Hanski, 1999), and these findings are also backed by empirical evidence (Hanski *et al.*, 1995; Hanski, 1999). Furthermore, as spatial clustering of habitat patches is beneficial to overall metapopulation persistence, spatial optimization of metapopulations is likely to have multiple local optima. This section aims to briefly explain the occurrence of multiple equilibria and multiple optima and their possible implications for spatially cost-effective species conservation strategies.

Biologists have found that many assemblages of plants and animals show a bimodal distribution of site occupation frequencies, i.e. the majority of species occur either in the majority of suitable sites or only in a few sites (see Hanski and

Gyllenberg, 1993 and references therein; Hanski *et al.*, 1995). Besides sampling effects and differences in specialization among species, the possibility of alternative equilibria is a plausible explanation suggested by metapopulation models. In many cases (see e.g. Levins, 1970; Hanski and Gyllenberg, 1993; Ovaskainen and Hanski, 2001), these models have one or more stable, positive equilibria, in addition to the so-called (stable or unstable) trivial equilibrium, where the species has gone extinct. The existence of stable positive equilibria other than the trivial equilibrium depends strongly on the characteristics of the species as well as the carrying capacity of the habitat patches (Hanski and Gyllenberg, 1993; Ovaskainen and Hanski, 2001). As environmental conditions change, equilibria can emerge or disappear and the metapopulation can shift from one equilibrium to another. Furthermore, observations (Hanski *et al.*, 1995) as well as theory (Hanski and Gyllenberg, 1993) indicate that these shifts can also take place for stochastic reasons.

Complex nonlinear dynamics in ecosystems (alternative equilibria, drastic ecosystem shifts) gradually receive more and more attention from economists (Perrings and Walker, 1997; Mäler, 2000). If an ecosystem is a complex dynamic system as analyzed in these papers, it is possible that instead of gradually changing in response to environmental perturbations, it can suddenly collapse to another equilibrium, after which it can be extremely difficult (and indeed costly) to restore its original state. As the literature on metapopulation dynamics shows that metapopulations can behave as complex dynamic systems, and that drastic shifts can occur in metapopulations (Hanski and Gyllenberg, 1993; Hanski *et al.*, 1995; Ovaskainen and Hanski, 2001), economic analysis of species conservation should be able to deal with these phenomena.

The possibility of sudden shifts between alternative equilibria in metapopulations could imply that there is a minimum spatial habitat quality below which the metapopulation has no positive stable equilibrium (see Figure 1). Therefore, for a species conservation strategy to be effective, its quality needs to be at least as high as where a bifurcation point exists and a positive stable equilibrium emerges (H_{min} in Figure 1). Furthermore, as stochastic factors play an important part in metapopulation dynamics, extinction can never be ruled out completely as a thriving metapopulation can still shoot below the bifurcation point by sheer chance.

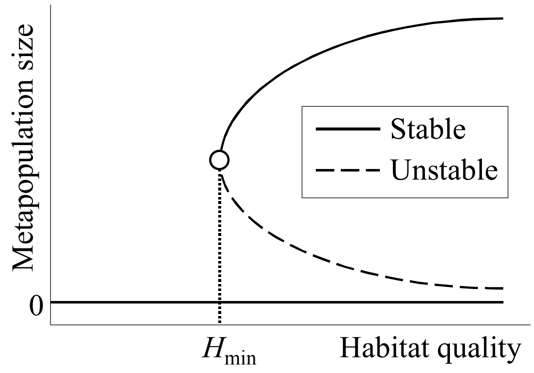

Figure 1: Possible relation between metapopulation size and quality of the spatial habitat configuration (based on Ovaskainen 2001). As empirical (Hanski *et al.*, 1995) as well as theoretical (Hanski and Gyllenberg, 1997; Ovaskainen and Hanski, 2001) analysis suggests, metapopulations can have multiple stable equilibria, two sets of which are depicted in this figure. Solid lines depict stable equilibria; the dashed line depicts unstable equilibria. For low values of the quality of the spatial habitat configuration extinction is the only stable equilibrium, but as the habitat quality increases a positive stable equilibrium emerges at the bifurcation point depicted by the empty dot in the graph.

Space adds another complexity to the problem, namely the occurrence of multiple optima. Intuitively, this effect is very similar to the occurrence of multiple optima in regional economic policy. In many economic sectors (e.g. large furniture shops) there are positive local externalities as consumers prefer to do their shopping in a location with a high number and diversity of shops. This tendency to spatially cluster firms leads to a situation where all shops are either in one location or another. Moving one shop to location A while all other shops remain in location B reduces total profits, even if location B would be superior to A if all shops moved to B.

Similar effects are likely to occur in spatial allocation of habitat in an area suffering from habitat fragmentation. Metapopulation theory tells us that every local population in a fragmented habitat will go locally extinct at some point in time. When it goes locally extinct, however, its habitat patch can be recolonized by individuals from occupied habitat patches in the vicinity of the vacated patch. Therefore, the metapopulation is more likely to persist if habitat patches are clustered spatially in order to preserve migration flows, just like furniture shops benefit from being close to other furniture shops. If a finite number of locations are suitable for clustering of habitat patches, there might be a local optimum for each suitable location.

Multiple equilibria and optima can have serious implications for the trade-off between species conservation and alternative land uses. First, if the metapopulation has some minimum habitat quality below which no positive stable equilibrium can exist, the production possibilities frontier of species conservation and alternative benefits should have an area where the marginal metapopulation size of forgone benefits are zero (the area between π_0 and π_1 in Figure 2). Second, multiple optima raise the possibility that several spatial conservation strategies are possible. For example, there could be two strategies: one where the possible metapopulation size, but also the minimum costs necessary to achieve the bifurcation point, are high (solid line in Figure 2) and one that is easier to achieve as the minimum costs to achieve the bifurcation point are lower, but the metapopulation size that can be achieved through this strategy is also lower (dashed line in Figure 2). Both the existence of a minimum habitat quality and several locally optimal strategies cause the production possibilities frontier of metapopulation size and the forgone benefits of conservation measures to be non-convex.

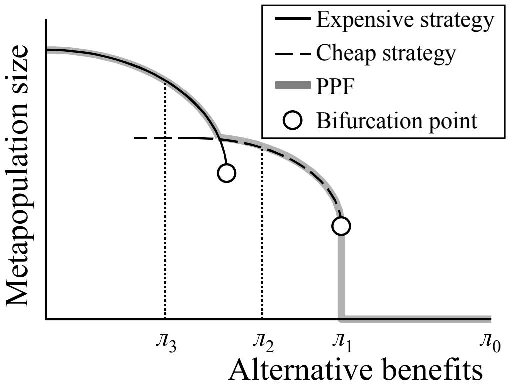

Figure 2: Non-convexities in the production possibilities set of metapopulation size and the alternative benefits of the resources used for conservation. As a minimum amount of forgone benefits is necessary to achieve any of the bifurcation points, there is an area where the marginal metapopulation size of forgone benefits is zero. Furthermore, as multiple optima might exist, several conservation strategies might be possible. Not only do these cause nonconvexities in the production possibilities set; they also might cause path-dependency of species conservation.

Third, the occurrence of multiple optima introduces a possible path dependency of species conservation. Suppose some small budget π_0 - π_2 is initially available for species conservation measures. In that case the “cheap” strategy in Figure 2 would be the only strategy yielding a positive stable equilibrium. Under a higher budget of, say, π_0 - π_3, the “expensive” strategy in Figure 2 is also possible, and it yields higher metapopulation size than the “cheap” strategy. Switching between the two strategies, however, might be difficult or very costly as it might imply that existing habitat or economic activity must be relocated. If such switching costs are high, therefore, species conservation might be locked in a suboptimal strategy such as the “cheap” strategy in Figure 2 if it is initially designed under a budget of π_0 - π_2 that is later on increased to π_0 - π_3.

3 Structure of the model

In order to demonstrate the possible effects of multiple equilibria and optima in a numerical example, I analyzed a number of spatially explicit settings with a bioeconomic optimization model. The general setting of the model is as follows. Suppose some area under consideration consists of a number of separate patches, and of each patch a part can be used as agricultural land or as habitat for some endangered species. A benevolent planner allocates these land use types, agriculture and habitat, over all patches such that some indicator of the benefits to the target species is maximized under a given minimum level of benefits from agricultural land. By maximizing the ecological objective for several different minimum agricultural benefit levels, a production possibilities frontier is constructed of protection of the target species and the alternative benefits of land used for this purpose, i.e. agricultural land use.

Assuming the forgone benefits of species conservation consist entirely of agricultural profits, the relation between spatial land use allocation and agricultural profits is described by a straightforward economic land use model. The relation between spatial land use allocation and species conservation is described by the incidence function model (IFM) (Hanski, 1994). From the size and location of all habitat patches p, the IFM calculates the probability that p is occupied, generally referred to as the incidence J_p. From the value of J_p for all patches one can in principle calculate a whole family of indicators, such as the expected number of occupied patches or the probability that at least one patch is occupied. This analysis indicates the benefits of species conservation by the expected number of occupied patches.

3.1 Linking agricultural profits to land use: a spatially explicit economic land use model

In the economic land use model each patch generates profits depending on transport costs and the distance between the patch and the farm. Let l denote land use types varying in agricultural and ecological characteristics, and let p denote patches varying in location. As each patch has a limited area a_p, the sum of the areas of land use types is equal to the area of the patch:

$$\sum_l A_{lp} = a_p \qquad \forall p, \tag{2.1}$$

where A_{lp} denotes the area of land use type l on patch p. For simplicity it is assumed that all patches have the same biophysical qualities, so that a land use type generates a revenue r_l per unit of area. The profitability of land use type l on patch p is equal to the revenue of l minus the transport costs:

$$\pi_{lp} = r_l - t_l d_p, \tag{2.2}$$

where π_{lp} denotes the profits per area unit of land use type l on patch p, t_l denotes the transport costs per distance unit of land use type l and d_p denotes the distance between patch p and the farm. Total profits Π are equal to

$$\Pi = \sum_l \sum_p \pi_{lp} A_{lp} . \tag{2.3}$$

3.2 The Incidence Function Model

The Incidence Function Model (IFM) was originally developed in order to provide a model that can provide guidance to quantitative questions about particular metapopulations, without having to use extensive simulation models that are tedious to construct and include many parameters that are hard to estimate (Hanski, 1994). The model assumes a finite number of patches that can be either ‘vacant’ or ‘occupied’. Vacant patches become occupied by colonization; occupied patches become vacant by extinction. Furthermore, the model assumes that the system converges to a quasi-steady state. A quasi-steady state is assumed instead of a steady state, because without a constant ‘source’ of individuals (an external mainland, as Hanski (1999) puts it) a finite metapopulation will ultimately go extinct. Before going extinct, however, the metapopulation may settle for a long time in a stable positive quasi-steady state.

Let J_p be the probability that patch p is occupied at any given time, generally referred to as the incidence of patch p. Let E_p be the probability that the population in patch p goes extinct, i.e. the probability that patch p becomes vacant given that it is occupied. Lastly, let C_p be the probability that patch p is colonized given that it is vacant. In equilibrium, the immigration rate and the extinction rate of patch p should be equal (Gilpin and Diamond, 1981):

$$J_p E_p = \left(1 - J_p\right) C_p . \tag{2.4}$$

Rearranging this equation yields equation (2.5):

$$J_p = \frac{C_p}{C_p + E_p}, \tag{2.5}$$

Hanski (1994) further elaborates on this function in order to develop a model that relates metapopulation dynamics to the quality of individual patches. In this model E_p depends on the area of the patch:

$$E_p = \min\left[\frac{\mu}{\left(H_p\right)^x}, 1\right], \tag{2.6}$$

where μ and x are coefficients, and H_p denotes the ecological area, i.e. the area corrected for ecological quality. The colonization probability C_p depends on the annual number of immigrants into patch p, denoted by M_p, and a parameter y that indicates the annual number of immigrants required for a colonization probability of 0.5:

$$C_p = \frac{M_p^2}{M_p^2 + y^2}. \tag{2.7}$$

The annual number of immigrants is determined by a weighted sum of the area of all occupied patches:

$$M_p = \sum_{q \neq p} \omega_q e^{-\alpha d_{pq}} H_q , \tag{2.8}$$

where ω_q denotes whether patch q is occupied, α is the rate of decrease of the number of dispersers per distance unit and d_{pq} is the distance[2] between patches p and q. Equations (2.5)-(2.8) form the basic structure of the IFM. Further analysis of the IFM, as well as directions on its estimation, can be found in, among others, Hanski (1994; 1999) and ter Braak et al. (1998). It has been applied to mainly animal species, varying from butterflies (Hanski, 1994) to forest mammals (Lawes *et al.*, 2000).

To enable economic optimization the incidence function model is modified in three ways. First, the migration function is modified in order to allow a static formulation of the model. The IFM is often applied in dynamic simulations, where the spatial metapopulation structure is calculated for up to a few thousand generations (see e.g. Hanski *et al.*, 1996; ter Braak *et al.*, 1998). In such simulations, values of the occupancy indicator ω_p are drawn at random in each generation such that $E(\omega_p=1) = J_p$. As for the static analysis in this paper we only need to know the stable positive quasi-steady state that results from the spatial habitat configurations, equation (2.8) is modified in order to get the equilibrium conditions of a quasi-steady state, replacing ω_q by the incidence J_q:

$$M_p = \sum_{q \neq p} J_q e^{-\alpha d_{pq}} H_q \,. \tag{2.9}$$

Second, assume ecological area H_p is a weighted sum of all land use types on the patch:

$$H_p = \sum_l v_l A_{lp} \quad \forall p \,, \tag{2.10}$$

where v_l denotes the ecological value of land use type l and A_{lp} denotes the area of land use type l on patch p. Third, as equation (2.6) includes a nonsmooth function that can cause problems in some optimization packages, an approximation of this function is used that is explained in Appendix A.

Many possible objective variables, such as the expected area of occupied habitat or the probability that the number of occupied patches remains higher than some minimum number can be too complex for the purposes of this analysis. As the main focus of this paper is the trade-off between species conservation and agricultural profits, the expected number of occupied patches is sufficient to express the ecological effect of conservation:

$$O = \sum_p J_p \,. \tag{2.11}$$

---

[2] In the original paper by Hanski (1994) d_{pq} is the border-to-border distance, but for simplicity we take the center-to-center distance.

3.3 Modeling procedure

The model is run using the non-linear programming algorithm CONOPT (Drud, 1985). Because the IFM has three equilibria when a stable positive equilibrium is possible, the system of equations consisting of eqs (2.5), (2.7) and (2.9) has three solutions: (i) the “trivial” solution where $J_p = C_p = M_p = 0$; (ii) an unstable equilibrium; (iii) the stable equilibrium that indicates the ecological performance of the solution. To make sure the model maximizes the number of occupied patches in the positive stable equilibrium, a starting position is calculated with IFM variable values for the positive stable equilibrium. Furthermore, as the problem is likely to have multiple optima, the model is run for several different sets of starting values and minimum profit levels.

4 Constructing production possibilities frontiers of agriculture and species conservation

Four analyses are done with the model: (i) calculation of a production possibilities frontier of species conservation and agricultural profits in a straightforward four patch configuration with no transport costs; (ii) calculation of a production possibilities frontier of species conservation and agricultural profits in a nine patch configuration, consisting of two clusters of patches, with no transport costs; (iii) calculation of a production possibilities frontier of species conservation and agricultural profits in the clustered nine patch configuration with transport costs of agriculture set at 1 ($t_{\text{agriculture}} = 1$); (iv) calculation of a production possibilities frontier of conservation of two different species under different minimum profit levels and in different spatial configurations. The parameter values of the model can be found in Table 1.

Parameter	Explanation	Value	
a_p	Patch area		2
r_l	Revenue	Agriculture	10
		Habitat	0
t_l	Transport costs	Agriculture	1 (Only in section 4.3)
		Habitat	0
μ	Extinction parameter		0.01
x	Extinction parameter		1
y	Colonization parameter		1
α	Migration parameter		2
v_l	Habitat value	Agriculture	0
		Habitat	1

Table 1: Parameter values used in the model

Two land use types are assumed: (i) agriculture with revenues to the farm, but no ecological value to the target species; and (ii) habitat with no revenues and high ecological value. It is assumed that all patches have the same size. In the model runs underlying sections 4.1, 4.2 and 4.4 transport costs are set at zero, whereas in the runs for section 4.3 transport costs t_l are set at 1 for agriculture. For the IFM generic parameter values as proposed by Hanski (1994) are used that should lead to reasonable results for butterfly metapopulations.

4.1 A straightforward spatial configuration

We start with a straightforward four patch square configuration as shown in Figure 3. Distances between the patches are calculated based on the co-ordinates of the patches, so the distance between, for instance, patch 1 and 2 is 1, that between patch 1 and 4 is √2.

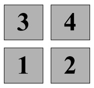

Figure 3: Straightforward four patch square configuration of patches

For this configuration production possibilities frontiers are calculated of the expected number of patches occupied by the target species and agricultural profits. To examine the effect of the distances in the model a frontier was calculated with distances 1.5 times as high as in the original run.

4.1.1 Results

The model results of this configuration are shown in Figure 4.

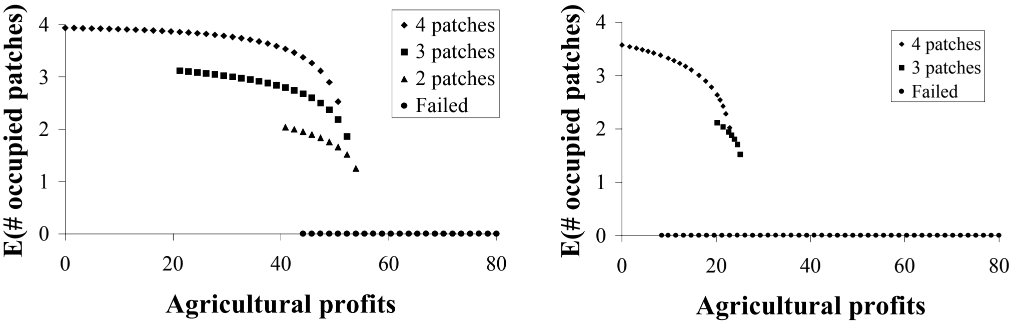

Figure 4: Left: Production possibilities frontier of species conservation (expressed as the expected number of patches occupied by the target species) and agricultural profits. Right: The same production possibilities frontier with distances increased by a factor 1.5.

Figure 4 shows that there are local optima in the problem that each refer to a different number of habitat patches. In the basic configuration one can maintain a positive stable equilibrium with either two, three or four habitat patches, but if the distances are 1.5 times as high the positive stable equilibrium cannot be maintained with a two-patch strategy. Furthermore, more agricultural land needs to be set aside to reach a stable positive equilibrium.

The results also show that although local optima with less than four habitat patches are possible, they are all dominated by a four patch optimum for most of the frontier: a higher expected number of occupied patches under the same profit level, or vice versa, can be achieved by creating four habitat patches. Therefore, the existence of multiple optima does not necessarily affect the convexity of the production possibilities frontier in this particular case. The existence of a bifurcation point, however, does introduce a similar non-convexity as the area between π_0 and π_1 in Figure 2. As the patches become more dispersed, the habitat areas – and hence the forgone agricultural profits – need to be larger to reach the bifurcation point.

4.2 A clustered configuration

We now turn to a somewhat more complex configuration of patches as shown in Figure 5. In this case there are nine patches, grouped in two spatial clusters. Again, distances between patches are calculated from the co-ordinates of the patches. So far there are no transport costs as these are investigated in section 4.3.

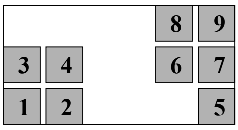

Figure 5: Clustered nine patch spatial configuration

The model is run maximizing the ecological objective for a number of different starting values and different minimum levels for agricultural profits.

4.2.1 Results

The results are shown in Figure 6.

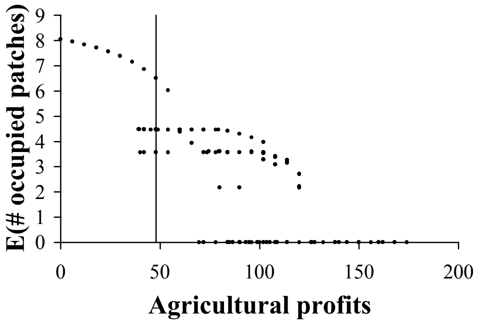

Figure 6: Production possibilities frontier calculated for the configuration shown in Figure 5 under zero transaction costs. The vertical line depicts an agricultural profits level of 48, of which three spatial configurations found are depicted in Figure 7.

At least three possible spatial conservation strategies can be distinguished in Figure 6. For example, at a minimum agricultural profits level of 48 three locally optimal configurations are found that are depicted in Figure 7: (a) distribution of habitat over all available patches; (b) concentration of habitat in the “large” cluster consisting of patches 5-9; and (c) concentration of habitat in the “small” cluster of patches 1-4.

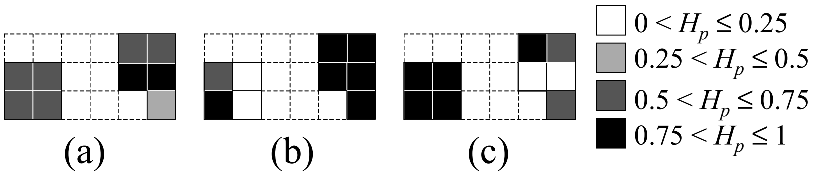

Figure 7: Spatial allocation of habitat in three optima found under a minimum profits level of 48. The optima refer to three different spatial conservation strategies: (a) distribute habitat over all patches (*O* = 6.5); (b) concentrate habitat in "large" cluster (*O* = 4.5); and (c) concentrate habitat in "small" cluster (*O* = 3.6).

Therefore, the general shape of the production possibilities frontier is likely to look as in Figure 8. The existence of multiple optima and multiple equilibria in the metapopulation as well as the possibility of sudden collapses of the metapopulation (empty dots in Figure 8) causes non-convexities in the production possibilities set of agricultural profits and species conservation.

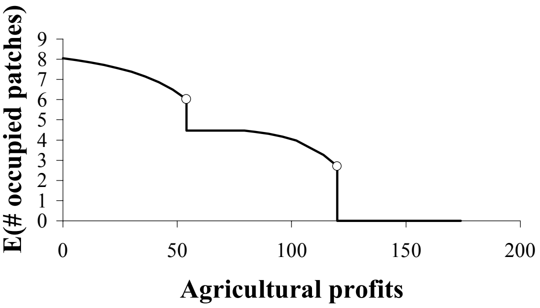

Figure 8: Production possibilities frontier of the expected number of occupied patches and agricultural profits.

4.3 The effect of transport costs in a clustered configuration

So far I excluded transport costs in the problem to gain insight in the non-linear and spatial ecological aspects first. In reality, however, location is an important determinant of the costs of conservation and an important consideration for farmers to select a particular patch for nature conservation. Therefore, I now turn to the effect of distance related costs t_l on the production possibilities frontier and the optimal spatial conservation strategy.

In this analysis I assume all patches belong to a farm located in the North Eastern corner of the area (black spot in Figure 9). As agricultural land use has some transport costs $t_{\text{agriculture}}$, distant patches such as 1, 2, 3 and 4 are less profitable for agriculture than areas close to the farm, such as patches 6, 7, 8, or 9.

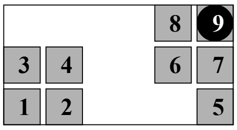

Figure 9: Location of the farm in the clustered nine patch spatial configuration

Therefore, we can expect that as far as the opportunity costs are concerned some patches become more suitable for habitat allocation as $t_{\text{agriculture}}$ increases. All other things being equal, one can expect at least two effects on the production possibilities frontier: (i) the frontier shifts inward as the land becomes less profitable; (ii) at a particular value of $t_{\text{agriculture}}$ some positive value of the ecological objective will be achieved regardless of the profits level because there is a certain area of unused land. This is, off course, assuming that no effort will be made to decrease transport costs or to make unused land profitable by, for example, non-agricultural land use.

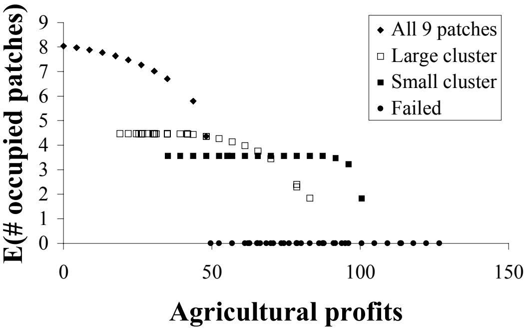

Figure 10: Production possibilities frontiers for three spatial conservation strategies under transport costs $t_{\text{agriculture}}$ equal to unity. As can be expected, the "small" cluster strategy becomes more attractive compared to the "large" cluster strategy as transport costs are higher for agricultural activity in the "small" cluster.

As Figure 10 shows, the maximum achievable profit level decreases (i.e., the production possibilities frontier shifts inward) as transport costs increase. Furthermore, it becomes worthwhile to concentrate habitat in the small cluster, as the patches in this cluster lie at a larger distance from the farm. With increasing transport costs the metapopulation can eventually persist at the maximum profits level, as some patches become unsuitable for agriculture.

4.4 An interspecies trade-off

So far the analysis focused on single species conservation, whereas the objective of nature conservation policy is often biodiversity conservation. Simply taking the number of species, however, often ignores the possibility that species have conflicting habitat requirements. For example, one species might depend on hedgerows for habitat, whereas others depend on pools. Therefore, whenever species have conflicting habitat requirements, policy makers also face a trade-off between species. Furthermore, if both species have comparable mobility and habitat size requirements (except, off course, whether the habitat is a hedgerow or a pool), it is likely that both species require a minimum quality of habitat configuration to reach the bifurcation point. The IFM-land use model can also provide insight in these trade-offs by the construction of production possibilities frontiers of the two species.

Analogously to the calculations in sections 4.1-4.3 the interspecies production possibilities frontiers can be constructed by maximizing the expected number of occupied patches of one species while keeping the expected number of occupied patches of the other species, as well as agricultural profits, at some minimum level. By doing so for different minimum levels of the ecological objective of the second species, an interspecies production possibilities frontier can be constructed. As the ecological model is nonlinear, however, it might be more efficient to maximize a weighted sum of both ecological objectives for a multitude of different weights under a minimum agricultural profits level. Therefore, the objective function is changed to:

$$O = \sum_s \sum_p w_s J_{ps} , \tag{2.12}$$

where O denotes the objective function, w_s denotes the weight of the species with $\sum_s w_s = 1$ and J_{ps} is the incidence of species s in patch p. The interspecies production possibilities frontier is constructed by maximizing O with $w_1 = 0, 0.02, 0.04, \ldots, 1$ and $w_2 = 1 - w_1$.

In order to isolate the effects of conflicting habitat requirements from other interspecies differences, I constructed production possibilities frontiers of two hypothetical species that depend on different habitat types, but have otherwise identical IFM parameter values.

4.4.1 Results for a simple four patch spatial configuration

Figure 11 shows the results for the simple four patch configuration under a minimum profits level of zero (left) and 20 (right).

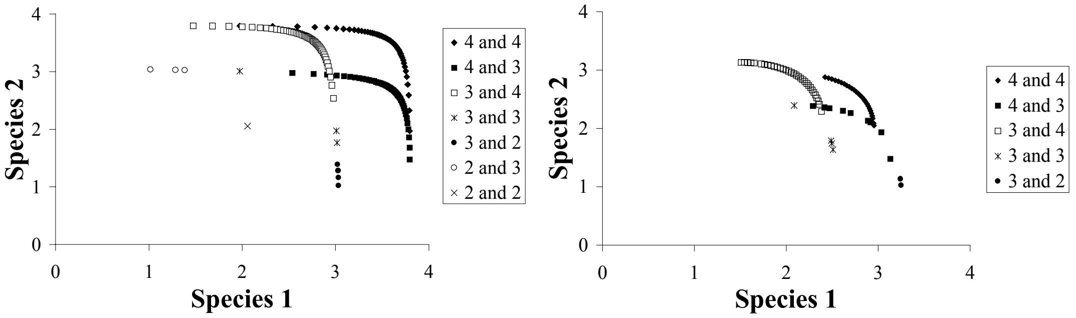

Figure 11: Interspecies production possibilities frontiers of two species that depend on different habitat types but are otherwise identical, in the simple four patch configuration. Left: results at a minimum profits level of zero. Right: results at a minimum profits level of 20.

These results seem to indicate that also in the interspecies production possibilities frontier distribution of habitat area over all patches yields the largest expected number of occupied patches. At a minimum profit level of 20, however, concentrating habitat in a few patches can be an efficient strategy if the species has a much lower value than the other species in the interspecies trade-off. If the species are valued more or less equally, distributing habitat of both species over all patches is probably still more efficient.

4.4.2 Results for a clustered nine patch configuration

In the nine patch configuration the problem apparently becomes very complex as a large number of local optima are found, as shown in Figure 12.

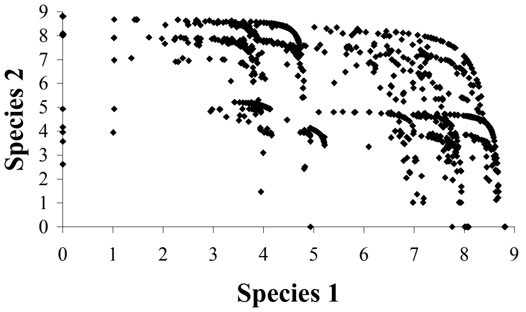

Figure 12: Production possibilities frontier of two species that depend on different habitats, but are identical in all other ecological aspects, in the nine patch clustered configuration.

Identifying all or most possible spatial conservation strategies in Figure 12 is quite impractical, but if we only look at the configurations behind the outer points, i.e. the points that constitute the actual frontier, we can still gain some insight in what is going on. Figure 13 shows the points in the actual frontier.

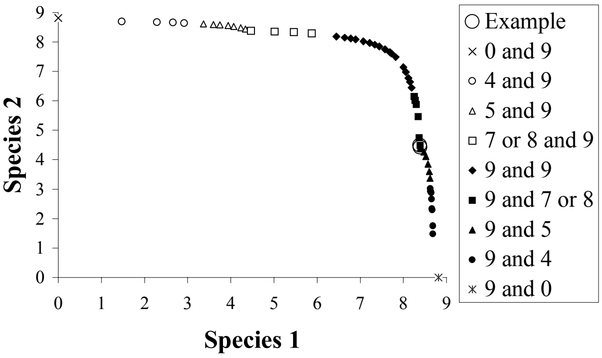

Figure 13: Outer points of the results presented in Figure 12, with an indication of the number of habitat patches per species in each point. The points highlighted under "Example" are presented in more detail in Figure 14.

Although the production possibilities set in Figure 12 seems to have only small nonconvexities, and the frontier in Figure 13 seems to curve smoothly, the configurations behind these points do not necessarily change gradually. Figure 14 shows the habitat configuration behind two points on the frontier highlighted by the empty circles in Figure 13. Although the points lie very close on the frontier, they differ strongly in spatial strategy: one distributes habitat of species 2 over both clusters (the strategy denoted as "9 and 7 or 8") and the other concentrates habitat in one of the two clusters (the strategy denoted as "9 and 5"). As the expected number of patches occupied by species 1 increases further, concentrating habitat of species 2 is more efficient than distributing its habitat over both clusters.

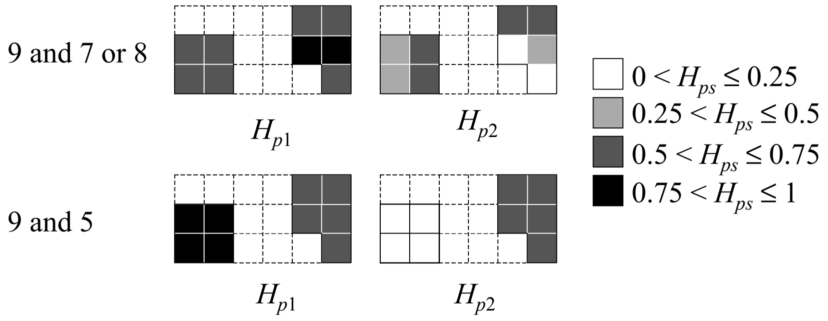

Figure 14: Configurations behind the points highlighted in Figure 13. As the expected number of patches occupied by species 1 is increased, concentrating habitat of species 2 (H_{p2}) in the larger cluster becomes more effective than distributing H_{p2} over the two clusters.

The results seem to confirm the conclusions for the four patch configuration in section 4.4.1 that concentrating habitat in a few patches can be an efficient strategy if the species has a much lower value than the other species in the interspecies trade-off.. Surprisingly, however, concentrating each species in another cluster seems to be very inefficient. Such strategies are compared with the production possibilities frontier in Figure 15.

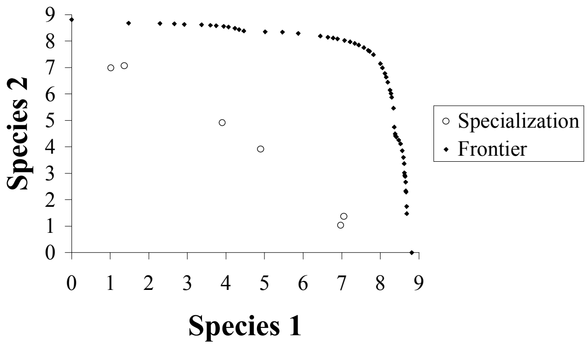

Figure 15: Concentrating habitat area of each species in another cluster (indicated as “specialization”) is unlikely to be an efficient strategy.

As Figure 15 shows, allocating habitat of each species in another cluster is dominated by strategies that distribute habitat area of at least one species over both clusters.

5 Discussion and conclusions

This paper presents an analysis of the effect of multiple equilibria and multiple optima in metapopulation dynamics on the production possibilities frontier of species conservation and alternative land uses. For this purpose, an integrated bioeconomic model of agricultural land use and metapopulation dynamics is used based on the Incidence Function Model (Hanski, 1994). The IFM has the ability to capture some of the nonlinear complexities in metapopulation dynamics, while still being relatively easy to implement in optimization analysis.

Production possibilities frontiers are constructed of agricultural profits and species conservation for four simple hypothetical spatial scenarios. In a simple four patch configuration the possibility to distribute habitat over all patches or to concentrate habitat in a few patches introduces locally optimal strategies, but it seems that the "concentrating" strategies are dominated by the "distributing" strategy. Therefore, it is not likely that the shape of the production possibilities frontier is seriously affected by local optima in this configuration. The fact, however, that some minimum quality of the spatial habitat configuration is required in order to maintain a positive stable equilibrium in the metapopulation introduces a non-convexity in the production possibilities set.

It is hardly surprising that more complex configurations can lead to more local optima. When spatial clusters of patches can be distinguished, locally optimal conservation strategies probably refer to concentration of habitat in some of the clusters or to distribution of habitat over all patches. This can easily lead to more non-convexities in the production possibilities set, especially if local differences in opportunity costs (e.g. because of transport costs) exist.

Path-depency of species conservation as mentioned in section 2 can also be found in the results. Take, for example, Figure 10. Suppose society would be willing to forgo agricultural profits such that about 80 units remain. Locating all habitat in the small cluster of patches would then be the only feasible strategy. Would the budget for species conservation increase subsequently, e.g. such that agricultural profits can decrease to about 40 units, we would have to relocate some of the habitat in the small cluster to the larger cluster to maximize the ecological objective. This, however, can be costly or even impossible in practice.

Interspecies trade-offs seem to depend in a similar way on spatial configuration and transport costs, but off course they also depend on interspecies differences. However, the analysis of interspecies trade-offs in clustered configurations turned out to a very complex matter, even for only two species and nine patches in a two-cluster configuration. Surprisingly, however, it does not seem to be efficient to concentrate habitat of each species in another spatial cluster of patches.

The results suggest that the shape of the production possibilities frontier is strongly affected by multiple equilibria and multiple optima in metapopulation dynamics, depending on the spatial configuration of candidate sites and transport costs. This finding underlines not only the importance of spatially explicit analysis, but also the use of ecological models capable of addressing these effects.

The interpretation of the results, however, does require some caution. First of all, the IFM is a probabilistic model, and the stable positive equilibrium (a quasi-steady state, as Hanski (1994) himself puts it) should be treated as a stable attractor rather than a deterministic steady state. For illustrative purposes such as done in this analysis, however, the 'deterministic' interpretation still yields intriguing results. Second, the analysis in this paper is done through numerical, quantitative methods, of which the results might depend strongly on the parameter values chosen. To generalize the results, more robust theoretical analysis is needed. Lastly, the reader might conclude from the results in sections 4.1 - 4.4 that distributing habitat area over several patches is generally better than concentrating habitat area in a few locations, keeping total habitat area constant. This, however, is a much-debated issue in ecology, also known as the SLOSS problem (Single Large Or Several Small), that is currently still far from being resolved. Ovaskainen (2002) provides an excellent overview of the SLOSS issue as well as an application of metapopulation theory to the problem.

Because the incidence function model is straightforward, easily estimable and yet well accepted in ecology, it is very suitable for spatially explicit bioeconomic analysis. The non-linearities in the incidence function model can complicate standard optimization, but this should not be regarded as a problem of the incidence function model. It is rather a problem of the process described by this model: multiple equilibria and optima are common phenomena in metapopulation ecology, and the incidence function model manages to capture these in a simple model.

The model can be extended in at least four directions. First, the economic module can be extended to describe farms more accurately. So far it is assumed that profits are generated directly from the patches, whereas in many agricultural sectors this is not true. For instance, dairy farms need land not only to produce fodder, but also for herding cattle. Therefore, the area of land a dairy farm can set aside for nature conservation without drastically changing farm management is limited.

The second possible extension is to include the institutional aspects that complicate nature conservation in agricultural areas in reality. Governments often face strong information asymmetries, enabling farmers to behave strategically (see e.g. Smith and Shogren, 2002). The government cannot observe the exact marginal profits of an agricultural patch, leaving the farmer some freedom to ask higher compensations than necessary. Furthermore, as the spatial configuration of conservation measures is an important determinant of the ecological success of the conservation strategy, the owner of an individual patch has more negotiating power if the surrounding patches are under conservation schemes already than if they are not. It would therefore be interesting to compare the outcome of the model presented in this paper with an extended version that includes these institutional aspects, in order to analyze the inefficiency they cause.

Third, addressing the stochastic aspects of the problem more explicitly can probably enhance the analysis. Instead of the expected number of occupied patches an indicator could be used that takes the stochastic nature of metapopulation dynamics more explicitly into consideration. For instance, the probability that the number of local populations (i.e., occupied patches) remains above some threshold can in principle be calculated from the incidences J_p, although as p increases this indicator eventually requires prohibitively extensive combinatorics to calculate.

Fourth, the numerical analyses in this paper have not yet been complemented with robust theoretical analysis. Although the IFM has been analyzed thoroughly by ecologists, more economic theoretical analysis of terrestrial metapopulation models is needed to gain insight in the trade-offs apparent in species conservation in agricultural landscapes.

References

Bink, R.J., Bal, D., van den Berk, V.M. and Draaijer, L.J., 1994. Toestand van de natuur 2. Report 4, IKC-NBLF, Wageningen, the Netherlands.

Briers, R.A., 2002. Incorporating connectivity into reserve selection procedures. Biological Conservation, 103:77-83.

Calkin, D., Montgomery, C.A., Schumaker, N.H., Polasky, S., Arthur, J.L. and Nalle, D.J., 2002. Developing a production possibility set of wildlife species persistence and timber harvest value. Canadian Journal of Forest Research, 32:1329-1342.

Conrad, J.M. and Salas, G., 1993. Economic strategies for coevolution: timber and butterflies in Mexico. Land Economics, 69:404-415.

Delbaere, B.C.W. (Editor) 1998. Facts & figures on Europe's biodiversity: states and trends 1998-1999. European Centre for Nature Conservation, Tilburg, The Netherlands, 332.

Drud, A., 1985. A GRG code for large sparse dynamic nonlinear optimization problems. Mathematical Programming, 31:153-191.

Gilpin, M.E. and Diamond, J.M., 1981. Immigration and extinction probabilities for individual species: relation to incidence functions and species colonization curves. Proceedings of the National Academy of Sciences, 78:392-396.

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

Hanski, I., 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology, 63:151-162.

Hanski, I., Pöyry, J., Pakkala, T. and Kuussaari, M., 1995. Multiple equilibria in metapopulation dynamics. Nature, 377:618-621.

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

Hanski, I. and Gyllenberg, M., 1997. Uniting Two General Patterns in the Distribution of Species. Science, 275:397-400.

Hanski, I., 1999. Metapopulation ecology. Oxford University Press, Oxford, UK, 266 p.

Hanski, I.A. and Gilpin, M.E. (Editors), 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, CA,

Hof, J. and Raphael, M.G., 1997. Optimization of habitat placement: a case study of the Northern Spotted Owl in the Olympic Peninsula. Ecological Applications, 7:1160-1169.

Holling, C.S., Schindler, D.W., Walker, B. and Roughgarden, J., 1995. Biodiversity in the functioning of ecosystems: an ecological synthesis. In: Perrings, C., Mäler, K., Folke, C., Holling, C.S. and Jansson, B.O. (Editors), Biodiversity loss: Economic and ecological issues. Cambridge University Press, Cambridge, pp. 44-83.

Lawes, M.J., Mealin, P.E. and Piper, S.E., 2000. Patch occupancy and potential metapopulation dynamics of three forest mammals in fragmented afromontane forest in South Africa. Conservation Biology, 14:1088-1098.

Levins, R., 1970. Extinction. In: Gerstenhaber, M. (Editor) Lectures on mathematics in the life sciences, Volume 2. American Mathematical Society, Providence, Rhode Island,

MacArthur, R.H. and Wilson, E.O., 1967. The theory of island biogeography. Princeton University Press, Princeton, 203 p.

Mäler, K.-G., 2000. Development, ecological resources and their management: A study of complex dynamic systems. European Economic Review, 44:645-665.

Margules, C.R. and Nicholls, C.I., 1988. Selecting networks of reserves to maximise biological diversity. Biological Conservation, 43:63-76.

Moilanen, A. and Cabeza, M., 2002. Single-species dynamic site selection. Ecological Applications, 12:913-926.

Opdam, P., van Apeldoorn, R., Schotman, A. and Kalkhoven, J., 1993. Population responses to landscape fragmentation. In: Vos, C.C. and Opdam, P. (Editors), Landscape ecology of a stressed environment. Chapman & Hall, London, United Kingdom, pp. 147-171.

Ovaskainen, O. and Hanski, I., 2001. Spatially structured metapopulation models: global and local assessment of metapopulation capacity. Theoretical Population Biology, 60:281-302.

Ovaskainen, O., 2002. Long-Term Persistence of Species and the SLOSS Problem. Journal of Theoretical Biology, 218:419-433.
Perrings, C. and Walker, B., 1997. Biodiversity, resilience and the control of ecological-economic systems: the case of fire-driven rangelands. Ecological Economics, 22:73-83.
Polasky, S., Camm, J.D., Solow, A.R., Csuti, B., White, D. and Ding, R., 2000. Choosing reserve networks with incomplete species information. Biological Conservation, 94:1-10.
Polasky, S., Camm, J.D. and Garber-Yonts, B., 2001. Selecting biological reserves cost-effectively: an application to terrestrial vertebrate conservation in Oregon. Land Economics, 77:68-78.
RIVM/CBS/WUR, 2003. Natuurcompendium 2003. National Institute of Public Health and the Environment, Statistics Netherlands and Wageningen University and Research Centre, Bilthoven/Voorburg/Wageningen.
Rohweder, M.R., McKetta, C.W. and Riggs, R.A., 2000. Economic and biological compatibility of timber and wildlife production: an illustrative use of production possibilities frontier. Wildlife Society Bulletin, 28:435-447.
Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. and Walker, B., 2001. Catastrophic shifts in ecosystems. Nature, 413:591-596.
Smith, R.B.W. and Shogren, J.F., 2002. Voluntary incentive design for endangered species protection. Journal of Environmental Economics and Management, 43:169-187.
ter Braak, C.J.F., Hanski, I. and Verboom, J., 1998. The incidence function approach to the modelling of metapopulation dynamics. In: Bascompte, J. and Solé, R.V. (Editors), Modelling spatiotemporal dynamics in ecology. Springer, Berlin, pp. 167-188.
van Zanden, J.L. and Verstegen, S.W., 1993. Groene geschiedenis van Nederland. Uitgeverij Het Spectrum B.V., Utrecht, The Netherlands.

Appendix A Smooth approximation of the extinction function

To run the model with a gradient-based optimization algorithm an approximation of the extinction function in eq. (2.6) is used. The extinction function is indifferentiable at

$$A = \mu^{1/x} .$$

This indifferentiability poses serious problems to most gradient-based optimization algorithms. Furthermore, we wish to allow the ecological area of some patches to become zero, but this would cause a division by zero in the extinction function. The extinction function can well be approximated by a differentiable function that allows A_p to be zero:

$$E_p = 1 - \frac{\sqrt{\left(\frac{\mu}{A_p^x + \varepsilon_1} - 1\right)^2 + \varepsilon_2} - \frac{\mu}{A_p^x + \varepsilon_1} + 1}{2} .$$

In this function ε_1 and ε_2 are small numbers that indicate the error in the approximation. The smaller the value of ε_1 and ε_2, the better the approximation of E_p, but at $\varepsilon_1 = 0$ divisions by zero can occur, and at $\varepsilon_2 = 0$ the function is non-smooth. In Figure 16 both error terms are equal to 0.01 for clarification, but they are 0.001 in the actual model runs.

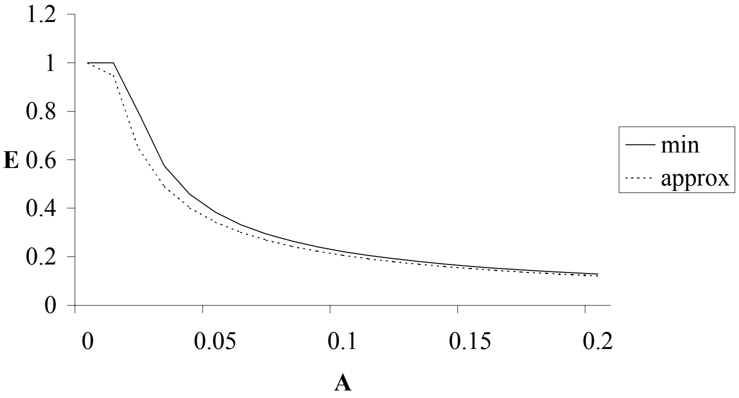

Figure 16: Approximation of the non-smooth function with error terms (see Appendix A) equal to 0.01