Optimizing spatial nature conservation in agricultural landscapes: an ecological-economic modeling synthesis

Rolf Groeneveld
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 focuses on the trade-off between agriculture and nature conservation in spatial planning of Western European agricultural areas. Because habitat fragmentation is one of the major causes of biodiversity decline in these areas, the spatial pattern of conservation measures is important for the ecological benefits of conservation. The spatial pattern of conservation measures also determines the costs of conservation, because the suitability of land for agricultural purposes - and hence the opportunity costs of conservation - varies strongly with location. Therefore, cost-effectiveness analysis of spatial nature conservation strategies must take their agricultural as well as their ecological effects into account.

Because monetary valuation of environmental benefits is problematic in many cases, cost-effectiveness, i.e. the minimum cost level for a prescribed goal, is often used in environmental economic studies instead of efficiency, which is the maximum difference between (monetary) costs and benefits. This paper presents a modeling framework to analyze the trade-off between agriculture and nature conservation in a particular area and to evaluate the cost-effectiveness of existing spatial nature conservation strategies, by the construction of a production possibilities frontier. Production possibilities frontiers have been applied in many economic analyses to gain insight in the trade-off between different, apparently conflicting, objectives. Furthermore, a production possibilities frontier can provide a useful benchmark to evaluate the cost-effectiveness of existing strategies, without making any attempt to express the benefits of nature conservation in monetary terms. In this case, the

---

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.
production possibilities frontier is constructed by maximizing the ecological objective under different minimum levels for the agricultural objective.

The ecological objective in this analysis is the expected number of patches occupied by a prespecified target species. The economic objective is the total profit level of all farms in the study area. The choice variable, i.e. the variable to be manipulated in order to construct the production possibilities frontier, is the spatial allocation of land use types.

The relation between the spatial allocation of land use and agricultural profits is described by a spatially explicit economic land use model. This model allocates land use types over several patches, such that the economic restrictions are met. The agricultural profits of a particular patch depend on the distance between the patch and the farm, the size and quality of the patch and the land use type.

The relation between the spatial allocation of land use and the expected number of occupied patches is described by a spatially explicit metapopulation model. For the purposes of this study a straightforward metapopulation model was needed that could provide a ranking of spatial conservation strategies based on their ecological benefits. Furthermore, the model should be able to handle discrete land units, in casu patches of land. In this study the Incidence Function Model (IFM) is used to relate the spatial land use pattern to the expected number of patches where a target species occurs. In the IFM the long-term probability that a particular patch is occupied depends on its quality, the probability that surrounding patches are occupied and the expected level of migration between patches, which depends on, among other, the distance between patches.

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

1 Introduction
Reports by the European Centre for Nature Conservation (Delbaere 1998) indicate that large numbers of known species in Western-Europe are threatened with local or global extinction. In the Netherlands, for example, the National Institute for Public Health and the Environment and the National Reference Centre for Nature, Forest, Landscape and Fauna reported sharp declines in specific species groups during the 20th century (Bink et al. 1994; RIVM 1997). 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. Much 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 (Opdam et al. 1993).

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 nature conservation 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, nature conservation) without unnecessary losses to others (say, agricultural income). Furthermore, many cost-effective strategies are possible depending on the desired level of nature conservation. To develop efficient nature conservation strategies, i.e. strategies that maximize net social welfare, insight is needed in the trade-off between agricultural profits and nature conservation.

This paper presents a spatially explicit bioeconomic model to develop cost-effective nature conservation strategies and to analyze the trade-off between nature conservation and agricultural income, with respect to the spatial configuration of nature conservation. The model combines economic land use modeling techniques and metapopulation theory. The metapopulation model used, the incidence function model (IFM) (Hanski 1994), has been applied in many ecological studies, is relatively easy to estimate and includes the basic mechanisms in metapopulations. This paper aims to analyze the effect of the spatial configuration of candidate sites, transport costs, and the ecological objective function chosen on the trade-off between species conservation and agricultural income. To do so, production possibilities frontiers are constructed of agricultural income and the expected number of habitat patches inhabited by a target species under two different assumptions regarding transport costs. The novelty of the paper is the integration of the IFM and economic land use modeling in a general framework of analysis. The strength of economic land use models is that they explicitly include the location of, and economic linkages between, patches of land. The advantage of the IFM is its applicability whereas it is generally accepted by ecologists as a predictive model.

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 the 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, however, not explicitly include economic considerations.

The paper proceeds as follows. Section 2 presents the mathematical structure of the model. Section 3 discusses the occurrence of multiple equilibria and multiple optima in the ecological model used. Section 4 demonstrates the model with two different optimization algorithms. Furthermore, this section discusses the possible effects of multiple optima and transport costs on the production possibilities frontier. Section 6 concludes.

2 Structure of the model

The model developed links two objectives, agricultural income and the expected size or viability of a metapopulation, to the spatial allocation of land use, which can include nature conservation as well as agricultural activity. The relation between spatial land use allocation and agricultural income is described by an economic land use model, whereas the relation between spatial land use allocation and the ecological objective is described by the incidence function model (Hanski 1994).

The model maximizes the expected number of patches inhabited by a target species under the restriction that the agricultural income is higher than a minimum. Given several different minima for agricultural income, a production possibilities frontier is constructed of agricultural income and the expected number of occupied patches.

The general setting of the model is as follows. The area under consideration consists of a number of separate patches, and each patch can be partly used for agricultural production or for biodiversity conservation. Each patch has its own size and suitability for agriculture or nature conservation, depending on its location. Within this area, we assume a benevolent planner allocates land use types over patches such that an ecological objective is maximized under a minimum agricultural income level.
### 2.1 Linking agricultural income to land use: a spatially explicit economic land use model

The agricultural model maximizes farm income by allocating land use types over a number of patches. Each patch generates profits depending on transport costs and the distance between the patch and the farm, and if transaction costs are very high distant patches become unprofitable. To some extent the model is similar to the classical von Thünen model, with the exception that transport costs include transport between patch and farm instead of transport to a central city. This is a reasonable assumption as on a regional scale the farm-patch distance is more relevant than the farm-city or the patch-city distance.

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 ($A_{lp}$) is smaller than or equal to the area of the patch:

$$
\sum_l A_{lp} \leq a_p \quad \forall p .
$$

(2.1)

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:

$$
\pi_{lp} = r_l - t_l d_p
$$

(2.2)

where $\pi_{lp}$ 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. Transport costs differ per land use type, for instance because growing maize or silage grass requires less transport than would grazing dairy cattle. Total income $I$ is equal to

$$
I = \sum_l \sum_p \pi_{lp} A_{lp} .
$$

(2.3)

### 2.2 The Incidence Function Model

The IFM was originally developed in order to provide a minimalistic 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. At equilibrium, the immigration rate and the extinction rate of patch \( p \) should be equal (Gilpin and Diamond 1981):

\[
\] (2.4)

Rearranging this equation yields equation (2.5):

\[
J_p = \frac{C_p}{C_p + E_p}, 
\] (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:

\[
E_p = \min\left(\frac{\mu}{A_p^{\mu}}, 1\right), 
\] (2.6)

where \( \mu \) and \( x \) are coefficients, and \( A_p \) 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:

\[
C_p = \frac{M_p^2}{M_p^2 + y^2}. 
\] (2.7)

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

\[
M_p = \sum_{q \neq p} \omega_q e^{-\alpha d_{pq}} A_q, 
\] (2.8)

where \( \omega_q \) denotes whether patch \( q \) is occupied, \( \alpha \) is the rate of decrease of the number of dispersers per distance unit and \( d_{pq} \) is the border-to-border distance 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. The value of \( \omega_q \) is not known in advance: all we know is that its
probability of being equal to unity is the incidence \( J_q \). Therefore, \( \omega_q \) is replaced by the incidence \( J_q \):

\[
M_p = \sum_{q \neq p} J_q e^{-\omega_q} A_q.
\]

(2.9)

Secondly, assume ecological area \( A_p \) is a weighted sum of all land use types on the patch:

\[
A_p = \sum_l w_l A_{lp} \quad \forall p,
\]

(2.10)

where \( w_l \) denotes the ecological value of land use type \( l \) and \( A_{lp} \) denotes the area of land use type \( l \) on patch \( p \). Thirdly, 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.

The ecological objective is defined as the expected number of habitat patches inhabited by the target species:

\[
O = \sum_p J_p.
\]

(2.11)

3 Multiple equilibria and multiple optima in metapopulations

Like many ecosystem processes, metapopulation dynamics are strongly nonlinear phenomena. Theory suggests that metapopulations can have multiple point equilibria, limit cycles, or more complex attractors (Hanski and Gyllenberg 1993; Hanski 1999). Multiple stable equilibria have also been encountered empirically in metapopulations (Hanski et al. 1995; Hanski 1999). Furthermore, as spatial clustering of habitat patches is beneficial to the overall metapopulation persistence, multiple local optima are likely to occur in spatial optimization of metapopulations.

The incidence function model also has at least two stable equilibria for a sufficiently high habitat quality (see Figure 1): one where the metapopulation has gone extinct and limited reintroduction of the target species will lead back to extinction, and one where the metapopulation is likely to persist. Starting with a metapopulation of some positive size, the incidence (the probability that the species is present at some point in time) decreases gradually with decreasing metapopulation persistence capacity. However, when the metapopulation persistence capacity becomes too low to maintain a positive metapopulation size (i.e., it has reached the bifurcation point depicted by the empty dot in Figure 1), the positive stable quasi-steady state disappears and the metapopulation collapses to the other stable equilibrium (i.e., it goes extinct). Such sudden collapse is similar to many other catastrophic events encountered in ecological nonlinear dynamics as explained in Scheffer et al. (Scheffer et al. 2001).
Besides multiple equilibria, multiple optima are also likely to occur in the model as clustering of habitat is beneficial to the ecological benefit function. Because habitat patches have a high colonization rate ($M_P$ in the incidence function model) if there are many local populations in the proximity, clusters of habitat have a higher metapopulation persistence than dispersed habitat patches. Therefore, a spatial cluster of habitat patches is an optimum: after all, moving one habitat patch away from the cluster decreases the metapopulation persistence. If several locations are suitable for clustering of habitat patches, there might be a local optimum for each suitable location. Similar phenomena can be found in spatial economics, where clustering of firms (e.g. furniture shops) leads to a situation where all shops are either in one location or another, but moving one shop to another location reduces total profits.

4 Economic optimization with the IFM

The model is run to investigate two questions: (i) the effect of nonlinearities in the incidence function model on the shape of the production possibilities curve; and (ii) the effect of transport cost on the shape of the production possibilities frontier.

The parameter values of the model can be found in Table 1. Two land use types are assumed: (i) an intensive land use type with high revenues and low ecological value and (ii) an extensive land use type with no revenues and high ecological value. It is assumed that all patches have the same size. In the model runs underlying section 4.1 transport costs are set at zero, whereas in the runs for section 4.2 transport costs $t_l$ are set at 1 for the intensive land use type. Hanski (1994) provides generic parameter values that should lead to reasonable results for butterfly metapopulations, and these values are used in this paper to analyze the integrated model.
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a_p$</td>
<td>2</td>
<td>$x$</td>
<td>1</td>
</tr>
<tr>
<td>$r_l$</td>
<td>Intensive</td>
<td>10</td>
<td>$y$</td>
</tr>
<tr>
<td></td>
<td>Extensive</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>$t_l$</td>
<td>Intensive</td>
<td>0; 1</td>
<td>$w_l$</td>
</tr>
<tr>
<td></td>
<td>Extensive</td>
<td>0; 0</td>
<td></td>
</tr>
<tr>
<td>$\mu$</td>
<td>0.01</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table 1**: Parameter values used in the model

The spatial configuration of patches is shown in Figure 2. There are nine patches, grouped in two spatial clusters. The farm that uses these patches is located in patch 9 in the North-Eastern corner of the area.

![Figure 2: Clustered nine patch spatial configuration](image)

The model is run by maximizing the ecological objective under the restriction that income remains higher than or equal to a minimum. By doing so for different minima on income and different starting values for the spatial allocation of land use, a production possibilities frontier is constructed that hopefully includes all local optima in the trade-off between agricultural income and ecological benefits.

### 4.1 The effect of multiple optima on the production possibilities frontier

To investigate the occurrence and effect of multiple optima the model is run maximizing the ecological objective for a number of different starting values and different minima for agricultural income. The results are shown in Figure 3.

![Figure 3: Production possibilities frontier calculated for the configuration shown in Figure 2 under zero transaction costs](image)

As Figure 3 shows at least three possible spatial conservation strategies can be distinguished: (i) distribution of conservation effort over all available patches; (ii) concentration of all conservation effort in the “large” cluster consisting of patches 5-
9; and (iii) concentration of all conservation effort in the “small” cluster of patches 1-4. These strategies become more visible if we look at the spatial conservation patterns behind the optima found at, for example, a minimum income level of 48 (Figure 4).

![Figure 4: Spatial allocation of conservation effort in three optima found under a minimum income level of 48. The optima refer to three different spatial conservation strategies: (a) distribute conservation effort over all patches \((O = 6.5)\); (b) concentrate conservation effort in “large” cluster \((O = 4.5)\); and (c) concentrate conservation effort in “small” cluster \((O = 3.6)\).]

Therefore, the production possibilities frontier is likely to look as in Figure 5. 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 5) causes non-convexities in the production possibilities set of agricultural income and species conservation. The policy implications of these non-convexities are discussed in further detail in Section 5.

![Figure 5: Production possibilities frontier of the expected number of occupied patches and agricultural income.]

**4.2 The effect of transport costs on the production possibilities frontier**

So far I excluded the spatial economic aspects of 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.

We can see in advance that if we increase \(t_l\), some patches become less profitable than others, and hence more suitable for nature conservation as far as the opportunity costs are concerned. 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 point some positive value of the
ecological objective will be achieved regardless of the income level because there is a certain area of unused land. This is, of course, assuming that no effort will be undertaken to decrease transport costs or to make unused land profitable by, for example, non-agricultural land use.

![Figure 6](image_url)  
**Figure 6:** Production possibilities frontiers for three spatial conservation strategies, under (a) zero transport costs; and (b) transport costs $I_{\text{invasive}} = 1$. 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 6a shows, the production possibilities frontier shifts inward as transport costs increase. Furthermore, it becomes worthwhile to concentrate conservation effort 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 income level, as some patches become unsuitable for agriculture.

### 5 Implications for policy

The analysis in Section 4 shows that the nonlinearities generally encountered in metapopulations can lead to nonconvexities in the production possibilities set of agricultural income and species conservation. The policy implications of these nonconvexities are twofold. First, it implies that society faces multiple optima in the social welfare function. Second, nature conservation policy could be locked in a suboptimal conservation strategy.

The problem of nonconvexities in the production possibilities set was already recognized as early as in 1920 by Pigou (1952). Figure 7 demonstrates the implications of nonconvexities in the production possibilities set of agricultural income and nature conservation under positive transport costs. The figure shows that the first order conditions for social optimality hold at three different points, each referring to a different conservation strategy. In this particular example it would be optimal to concentrate conservation effort in the smaller cluster of patches, but the indifference has to be only slightly different to make it more desirable from a social point of view to distribute conservation effort over all patches. It is likely that more realistic settings will have a multitude of optima, making it even more difficult to find the globally optimal conservation strategy.
The second policy implication of nonlinearities in metapopulation dynamics is also concerned with the choice between alternative conservation strategies. It is possible that under one budget restriction specialization of clusters in either agriculture or conservation is optimal, whereas under a larger budget it is better to establish some of each land use type in each cluster.

Consider the three conservation strategies in Figure 7. Suppose some budget is available to compensate farmers for income losses caused by nature conservation. Starting from a small budget, conservation policy would optimally concentrate all conservation effort in the small cluster, as this would be the only strategy that yields a positive metapopulation size. As the budget is increased, additional conservation effort would have little effect as it takes place in the other cluster. When net agricultural production is reduced to $I_2$, it would theoretically be better to shift all conservation effort to the larger cluster of patches if such a move would have no ecological or economic effects. In reality, however, these effects would be huge, keeping conservation policy effectively locked in a strategy that is optimal for small, but suboptimal for large budgets.

6 Discussion and conclusions

This paper presents an integrated bioeconomic model of agricultural land use and metapopulation dynamics. With this model production possibilities frontiers are constructed of agricultural income and species conservation for a simple hypothetical spatial scenario in order to compare two optimization algorithms and to demonstrate the effect of nonlinearities in metapopulation dynamics on the production possibilities frontier.

The results suggest that the shape of the production possibilities frontier depends strongly on the spatial configuration of candidate sites, ecological objective and transport costs, which underlines the importance of spatially explicit analysis. More specifically, the results indicate that the occurrence of multiple optima in metapopulations is of particular importance to spatial conservation policy. As Figure 7 shows, multiple optima can cause non-convexities in the production possibilities set,
which in turn can lead to multiple social optima. Furthermore, the occurrence of multiple optima can lead to path-dependency in the cost-effectiveness of spatial conservation strategies.

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 two 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 income 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 analyse the inefficiency they cause.

References


**Appendix A Smooth approximation of the extinction function**

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

$$ A = \mu^{\epsilon_\mu}.$$ 

This indifferentiability poses serious problems to most gradient-based optimisation 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:

$$ E_p = 1 - \frac{\left( \frac{\mu}{A_p + \epsilon_1} - 1 \right)^2 + \epsilon_2 - \frac{\mu}{A_p + \epsilon_1} + 1}{2}. $$

In this function $\epsilon_1$ and $\epsilon_2$ are small numbers that indicate the error in the approximation. The smaller the value of $\epsilon_1$ and $\epsilon_2$, the better the approximation of $E_p$, but at $\epsilon_1 = 0$ divisions by zero can occur, and at $\epsilon_2 = 0$ the function is non-smooth. In Figure 8 both error terms are equal to 0.01 for clarification, but they are 0.001 in the actual model runs.
Figure 8: Approximation of the non-smooth function with error terms (see Appendix A) equal to 0.01