

A model-based approach for designing cost-effective compensation payments for conservation of endangered species in real landscapes

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Abstract:

An approach is present which integrates an economic and an ecological model for designing cost-effective compensation payments for conservation of endangered species in real landscapes. The approach is used to develop a cost-effective payment scheme for conservation of an endangered butterfly species (*Maculinea teleius*) protected by the EU Habitats Directive in the region of Landau, Germany. Although the results from our case study are specific to the area and species studied, the methodology is general and applicable elsewhere. The results of the case study are used to analyse the effect of metapopulation dynamics on the cost-effectiveness of payment schemes, to compare spatially homogeneous and heterogeneous payments, and to evaluate an existing conservation scheme.

Key words:

Conservation, biodiversity, metapopulation dynamics, cost-effectiveness, ecological-economic modelling spatial heterogeneity

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I. Introduction

Conservation of endangered species is demanded by legislation in many parts of the world. Examples of such legislation are the Endangered Species Act of 1973 in the USA and the European Union Habitats Directive of 1992. Some of the species protected by such legislation require reserves in order to survive, but others require particular types of human land use to be carried out on a regular basis. Such human land-use was often profitable in the past, but today, due to technological and economic development, this is no longer the case. For example, much of the biodiversity-rich land in the EU depends on low-intensity farming which is no longer economically viable (Bignal and McCracken 2000). As the political will often exists that landowners should not be forced to carry out a certain type of land-use, they have to be compensated (Bromley and Hodge 1990, Hanley et al. 1998). Experience with the USA Endangered Species Act has also shown that forcing owners of land with endangered species to carry out conservation measures may encourage them to try and eradicate the species concerned in order to avoid the conservation costs (Brown and Shogren 1998). Compensation payment schemes for biodiversity enhancing land-use measures now play an important part in conservation efforts in Europe, the USA and other parts of the world, particularly in the context of agri-environmental policy. Examples of such schemes include the Countryside Stewardship and the Moorland schemes in the UK (Hanley et al. 1998), nature protection contract schemes (Vertragsnaturschutzprogramme) in Germany (Hampicke and Roth 2000) and the Fish and Wildlife Service Spending on endangered species recovery in the USA (Simon et al. 1995).

So far, relatively little research has been carried out with respect to the cost-effectiveness of compensation payment schemes, i.e. with respect to their ability to achieve a maximum conservation output for a given financial budget. One reason may be that addressing the scheme's cost-effectiveness requires the integration of knowledge from ecology and economics, and that with respect to the evaluation of conservation policies, such interdisciplinary work has evolved only recently.

Examples of such work include Ando et al. (1998) and Polasky et al. (2001) who address the problem of cost-effective reserve site selection and analyse the extent to which improvements in efficiency can be achieved by integrating economic costs (land prices) into the selection criteria of conservation sites compared to an approach that only considers ecological parameters such as the number of endangered species. Another example is Lichtenstein and Montgomery (2003) who estimate the location of a production possibility frontier for timber production and the conservation of terrestrial invertebrate species on a forested landscape.

With regard to the instrument of compensation payments Hanley et al. (1998) as well as Oglethorpe and Sanderson (1999) integrate an economic and an ecological model and generate quantitative data of the costs and benefits of certain specific conservation measures. The combined ecological-economic models are able to determine the benefits and the costs of conservation measures (and thus the necessary compensation payments) simultaneously, but do not address the issue of how to allocate conservation measures cost-effectively.

Johst et al. (2002) combine economic data, an ecological model and a numerical optimisation procedure and quantitatively determine cost-effective compensation payments for species conservation which are differentiated in space and over time. To illustrate the operation of their approach they apply it to the design of a compensation payment scheme for the protection of the White Stork (*Ciconia ciconia*) in a hypothetical landscape. This research shows how cost-effective compensation payments may be developed in principle, but the hypothetical case study is rather simple, and neglects many complexities that are relevant for the development of cost-effective compensation payments for real conservation problems.

The aim of this paper is to further develop the research regarding the cost-effectiveness of compensation payments for biodiversity conservation measures. We do this with the help of a case study: the development of a cost-effective payment scheme for the conservation of an endangered butterfly species (*Maculinea teleius*, protected by the EU-Habitats Directive) in the region of Landau,

Germany, a spatially structured agricultural landscape. The paper advances the research on the cost-effective design of compensation payments in four areas:

(1) *Designing a modelling approach for cost-effective payments in a real landscape:*

We go beyond Johst et al. (2002) as the paper aims at developing an ecological-economic modelling approach for designing cost-effective compensation payment schemes for species conservation in real landscapes. The landscape data were obtained from the GIS analysis of a satellite image. Furthermore, in Johst et al. data on conservation costs were gained through a survey of farmers who were aware that the data were collected solely for scientific research. The survey method is problematic if the farmers know that the data is used for designing actual payments as then they have an incentive to answer strategically. To avoid such problems in the present study, costs are calculated through the method of standard gross margin calculations.

(2) *Analysing the influence of metapopulation dynamics:*

The butterfly population exhibits *metapopulation dynamics*, which means that the local dynamics of the butterflies in the individual meadows interact through the exchange of individuals. This interaction usually leads to a mutual stabilisation of the local populations and – in case local populations go extinct – may lead to the re-colonisation of empty meadows (e.g. Hanski 1999). The influence of metapopulation dynamics on optimal land-use decisions has been thoroughly analysed in ecology. However, with a few exceptions (e.g. Bulte and van Kooten 1999, Groeneveld 2004) their influence has not been analysed from an economic point of view. The present case allows for a discussion regarding how the existence of metapopulation dynamics affects the cost-effective design of compensation payments for conservation measures.

(3) *Spatial heterogeneity of compensation payments:*

It has been emphasised in the literature that conservation measures should be spatially heterogeneous if benefit functions (e.g. Babcock et al. 1997, Wu and Bogess 1999, Wätzold and Drechsler 2005) and cost functions (e.g. Innes 2000, Smith and Shogren 2002) spatially differ. We compare the cost-effectiveness of spatially homogeneous and heterogeneous payments for the

case study and analyse how much the cost-effectiveness of compensation payments may be improved if spatially heterogeneous benefits (a) and costs (b) are taken into account.

(4) *Evaluation of existing payment scheme:*

The case study contributes to the evaluation of existing conservation policies. A payment scheme for biodiversity-enhancing land use measures exists in the region of Landau and we use the ecological-economic modelling approach to analyse the scheme's contribution to *Maculinea* conservation.

The paper is structured as follows: Section 2 introduces the conservation problem and its relation to different types of land use in the region of Landau. Based on knowledge of the butterflies' requirements for survival in the landscape, alternative land use strategies are suggested. Following these considerations, the model-based approach that determines cost-effective land use strategies and compensation payments to achieve them is described. The approach consists of three components that are presented in the following sections. The economic model that is introduced in Section 3 determines the costs of alternative land use strategies for each meadow as well as the overall costs and the compensation payments necessary to induce land users to adopt these strategies. The cost structure – together with the conservation budget - shapes the land use and the spatio-temporal structure of the landscape in the region. The ecological effects of the alternative land use strategies are determined by an ecological model describing the metapopulation dynamics of the butterflies in the landscape (Section 4). This model is first analysed in a simple and fictitious landscape which disregards the spatial differentiation of costs and benefits, but allows for gaining some general understanding of the effects of different land use strategies on the survival of a *Maculinea* metapopulation. In Section 5, the ecological and economic components of the problem discussed in Sections 3 and 4 are considered in an integrated manner to identify cost-effective land-use strategies and the corresponding compensation payments. These are defined by maximising the viability of the butterfly metapopulation for a given budget. In Section 6 the model results are discussed.

2. Land-use and conservation of *M. teleius*

Maculinea teleius is a meadow-dwelling butterfly that relies on the presence of open landscapes. Most adults fly in the weeks of July and lay their eggs on the plant *Sanguisorba officinalis*. Larvae are adopted by ants of the species *Myrmica scabrinodis*. Both plant and ant species are found only if a meadow is mowed in a certain way. This implies that the survival of the butterfly *M. teleius* strongly depends on when and how often meadows are mowed.

The dependence of *M. teleius* on a certain type of mowing largely explains why the butterfly was quite common in Germany until the 1950s, but since then its population size has steadily declined. In former times meadows were used rather extensively. In particular, the meadows of a region were not mowed all at once but the mowing season extended over the whole summer. Therefore, even if some meadows were unsuitable for the butterflies at a particular time, enough other suitable meadows were available to which butterflies could disperse and deposit their eggs. Today in contrast, all meadows in a region typically are mowed simultaneously twice a year with the first session being at the end of May and the second session six to eight weeks later. This mowing regime (henceforth referred to as the “conventional mowing regime”), however, is relatively unsuitable for the reproduction of the butterflies as, in particular, the second session of mowing falls exactly into the weeks during which the butterflies deposit their eggs on the *Sanguisorba* plants.

The concentration of mowing on two points in time maximises the farmer’s profit and has been made possible due to the development of machinery which allows mowing of a large area within a short period of time. In order to induce farmers to adopt a mowing regime that is more beneficial to the butterflies, the farmers have to be compensated.

In the present paper a cost-effective compensation payment scheme for a region east of the town of Landau in the Rhine Valley is developed. Our geographic data base comes from a digitised satellite image of this area (10 by 6 km² with a resolution of 20 by 20 m²). The image allows one to distinguish between 14 different landscape types in each pixel, such as settlements, traffic ways, lakes and rivers, forests, meadows, arable land, etc. For the ecological model below we structure

the 14 landscape types into four main types as they are experienced by the species: meadows, open land (e.g., traffic ways, lakes and rivers, arable land), forests (including shrubland), and settlements. Figure 1 shows the model landscape.

Having identified the individual meadows (whose total number is 347) in the landscape, their areas a_i are determined by counting the pixels belonging to each meadow. The location of each meadow is defined by its midpoint, or centre of weight, such that the x (y) - co-ordinate of a meadow is the average of the x (y) - co-ordinates of all pixels belonging to that meadow. From these x - y locations the Euclidian distances, $d_{ij} = ((x_i - x_j)^2 + (y_i - y_j)^2)^{1/2}$ are calculated for all pairs (i, j) of meadows. The meadow sizes are required as an input into the ecological as well as the economic model, whereas the pair-wise distances are only needed as an input into the ecological model.

A large variety of alternative mowing regimes is considered. A mowing regime is coded by three numbers, x - y - z . The first number tells whether a meadow is mowed every year ($x=1$) or every second year ($x=2$). The second number, y , ($y=-1, 0, \dots, 12$) consecutively codes the week of the first mowing where -1 stands for the second to the last week of May, 0 for the last week of May, and so on. After being mowed, a meadow may or may not be mowed a second time, namely 4, 6, or 8 weeks later, which is coded by $z=4, 6, \text{ or } 8$, respectively. If a meadow is not mowed a second time, this is indicated by $z=0$. For instance, the conventional mowing regime introduced above then is coded as (1,0,6). Altogether, we consider $2 \times 14 \times 4 = 112$ different mowing regimes.

It is assumed that a conservation agency selects one of the 112 mowing regimes and offers a certain payment to farmers. The farmers either accept the payment and adopt the selected mowing regime (henceforth denoted as the “promoted mowing regime”) or stick to the conventional one. Whether the promoted or the conventional mowing regime is adopted on each individual meadow is determined by the economic model.

3. Economic model

3.1 Model description

The aim of the economic model is to determine the compensation that has to be paid to induce a farmer to adopt a certain promoted mowing regime. We assume that the size of this compensation is determined by three components: (I) Compensation for the foregone profit that arises because the farmer cannot carry out the profit-maximising mowing regime, (II) compensation for the farmer's transaction costs arising from scheme participation, and (III) the farmer's personal attitude towards conservation.

(I) To determine the compensation payments for the foregone profit in adopting alternative mowing regimes for farmers, the method of standard gross margin calculations (see e.g. Hodgson et al. 2005) has been used. We give a brief description of how the field specific compensations have been calculated. A detailed description of the calculations and how the underlying assumptions are derived can be found in Bergmann (2004).

In the region of Landau, grassland is used intensively in dairy and cattle production. Farmers usually harvest silage (or less frequently hay) with a first cut approximately at the end of May, a second cut about six weeks later and a third cut in August/September. As an alternative to the third cut, the grassland is often used for grazing. The most important factor that determines the quality of the silage and the hay is its energy content, which is maximised by the prevalent mowing regime in the region.

For this reason, the reduction in energy yields per ha that is caused by the different mowing regimes compared to the prevalent mowing regime forms the basis of the calculations of the payments for the foregone profits. As most farmers use silage, the calculations are based on silage production. The impact of the various mowing regimes on the energy content of silage have been determined on the basis of a literature review on data from relevant field research. In general, the energy content of the silage, and thus its quality as fodder continuously decreases the later the date

of the first mowing is. Quantitative calculations of the energy loss have been based on functions estimated by Opitz von Boberfeld (1994, 262).

We assume that the farmers purchase concentrates as an additional fodder to compensate for the loss of energy yields in the silage and calculate the compensation payments accordingly. However, due to its low quality, silage harvested with a first cut in August can no longer be used in cattle nutrition. Therefore, for mowing regimes with a first cut later than the beginning of August, we assume that farmers have to be compensated for the complete loss of usability of the meadow for cattle nutrition.

The energy yields of the various mowing regimes (including the conventional one) on each meadow have been estimated based on information about medium grassland yields in the region taking into account three variables: Soil quality and soil humidity, which have a positive influence on productivity, and altitude, which has a negative influence. All variables are relatively homogenous throughout the study region. Soil quality number is about 35, the humidity level is “high” (as compared to “low”), as the region can be regarded as riparian, intersected by several rivers, and the altitude is below 250 msl.

We further take into account variable costs of the various mowing regimes such as costs for transport, machinery and fertiliser. A part of these costs (calculated on a per hectare basis) decreases with an increase in meadow size. Therefore, we distinguish between three meadow sizes ($a < 0.75\text{ha}$; $0.75\text{ha} < a < 1.5\text{ha}$; $a > 1.5\text{ha}$) and assume different variable costs for the three sizes. The meadow size as well as the soil quality number, the humidity level and the altitude are known for each individual meadow and stored in the data base described in Section 2.

The necessary compensation for the foregone profit is then calculated for each mowing regime and each meadow taking into account the necessary purchase of concentrates, and, if necessary, other additional fodder and the variations in variable costs.

(II) There are different types of transaction costs that arise for a farmer if he or she participates in a compensation payment scheme. The farmer has to gather information about the scheme, fill

out administrative documents and spend some time with the conservation manager in case the farmer's compliance with the scheme's requirements is monitored. The farmer needs to be compensated for the transaction costs to provide sufficient incentives for participation. Such compensation is common practice in EU agricultural schemes and in line with such practise we estimate the compensation to be 100€ per ha.

(III) In the decision to adopt the promoted mowing regime, the farmer's personal attitude towards the conservation objective plays a role, too. This attitude is described by a utility u where a positive u represents a farmer who draws a personal benefit from the conservation objective and a negative u represents a farmer who shows an aversion to the conservation programme, irrespective of financial compensation (cf. Smith and Shogren 2002). Obviously, it is difficult to get information about the distribution of u . Therefore, we assume that for each meadow u is a uniform random variable $u \in [-u_0, +u_0]$ with values for u_0 of 50€, 100€ and 200€.

3.2 Model analysis

To determine the mowing regime on a given meadow, a value for u is drawn from the distribution and the promoted mowing regime is adopted if the compensation payment $p > c + a + u$, where c represents the foregone profit and a the incentive component to participate in the scheme. We assume that all participants receive the same payment which is the common approach of many payment schemes in the EU and also of the existing scheme in Landau. The total amount of money that has to be spent by the agency is the total area of all meadows with the promoted mowing regime (in ha) multiplied by the payment.

To determine p for a given budget B (the amount of money that can be spend on conservation in the region of interest) we start with $p = 1\text{€}/\text{ha}$ and successively increase the payment in steps of $1\text{€}/\text{ha}$. In each step we determine which meadows adopt the promoted mowing regime and determine how much the agency has to spend for these meadows. We proceed until this amount is just below the budget B , such that in the next step the budget would be exceeded. The result is the payment that leads to maximum possible exhaustion of the available budget B . The difference

between B and the actual amount of money spent is negligible within the scope of the analysis. Next to p , the analysis determines which individual meadows adopt the promoted mowing regime as well as the total area A of such meadows.

As the decision to adopt the promoted mowing regime on a given meadow depends on the random incentive u , payment p and total area A are random, too. To account for this randomness, costs for all meadows are sampled randomly 10 times. Each time the compensation payment and the total area adopting the promoted mowing regime are determined and an average is taken over the 10 replicates.

3.3 Results

Figure 2a shows the costs of various mowing regimes for a meadow of 1 ha size. For smaller or larger meadows the curves look very similar but are shifted up- or downwards respectively. As expected, the costs of a mowing regime increases with the week of (first) mowing, because the later the mowing in the year the higher the loss of energy yields in the silage. Besides, if the first mowing is early (before week 7, i.e. third week of July), costs are higher the less frequently the meadow is mowed: costs are lowest if the meadow is mowed twice every year (dashed line without dots), highest if the meadow is mowed only once every second year (solid line with dots) and in between if meadows are mowed once every year or twice every second year. This is partly different if the week of the first mowing is week 7 or later, which is due to a sharp increase in the costs of the mowing regimes with two mowings (dashed lines). That increase is caused by the fact that if the first mowing is too late, the second mowing will be so late (end of August or later) that the harvested grass has no economic value for the farmer at all. As expected, the more expensive a mowing regime the smaller the (expected) total meadow area in the landscape which adopts that mowing regime for a given budget (Fig. 2b).

4. Ecological model

4.1 The local dynamics

The local dynamics of the butterfly *M. teleius* on each individual meadow is dependent on two

resources: Plants of species *Sanguisorba officinalis* for egg deposition and ant nests (species *Myrmica scabrinodis*) for pupation. As we concentrate on the impact of mowing, the life cycle is modelled as simple as possible and follows in principle the model of Hochberg *et al.* (1992). The model used in this study is a stochastic simulation model. Details are described in Johst *et al.* (subm.) and here only a brief overview of the model is given.

The life of the butterfly (Thomas and Settele 2004) is divided into an over-ground phase on the meadow and an underground phase in the ant nests. The over-ground phase encompasses approximately three months (June, July and August) and is considered on a weekly scale, and the underground phase includes nine months considered as one whole period. The over-ground phase involves the eclosion of adults followed by egg deposition and death of adults, and the development of three different larvae stages on the *Sanguisorba* plants. All larvae which get older than 3 weeks successively fall to the ground where they are adopted by the ants. The underground phase in the ant nests includes three processes: (1) larval survival due to the winter mortality of ant nests, (2) intra-specific competition for food in the ant nest characterised by so-called scramble competition and (3) survival after possible parasite infestation. Then the life cycle switches to the over-ground phase again.

Mowing influences the population dynamics in a direct and an indirect way. The direct effect is that during a mowing event eggs and larvae that are currently on the *Sanguisorba* plants are destroyed, and that the abundance of *Sanguisorba* will be insufficient for egg deposition for the next four weeks. The indirect effect of mowing (Thomas 1984) is that it stops succession of the vegetation of the meadow, i.e. keeps the meadow open and the composition of plant species relatively constant. If, e.g., meadows are mowed too rarely (less than once in two years) the abundance of *Sanguisorba* declines. Similarly, rarely mowed meadows with thick vegetation become unsuitable for *M. scabrinodis* whose abundance declines with too infrequent mowing. On the other hand, field data show that too frequent mowing harms the ants as well, so the mowing frequency that maximises the abundance of ant nests is once per year.

4.2 The landscape dynamics and the dispersal model

As described in Section 2, each meadow in the landscape is either mowed in the conventional way or according to the promoted mowing regime. The local dynamics on the individual meadows are coupled in the landscape through the dispersal of butterflies among different meadows which leads to metapopulation dynamics. The dispersal model describes the emigration of butterflies from their “home”, or “source”, meadow as well as their movement to other patches which includes the possibility of dying, e.g., due to predators, during the flight.

Emigration of the butterflies to deposit their eggs on a meadow different from their eclosion location, depends on the quality of the meadow i.e. on the abundance of the *Sanguisorba* plants (see above). Based on field observations, we assume that the butterflies emigrate with a high probability (0.9) if the habitat quality is low; otherwise there is only little emigration (0.1). The decision to emigrate is made after eclosion on a weekly time scale leading to a certain number of butterflies leaving the meadow.

Now it has to be determined which of these emigrants reach which of the other meadows. The share of emigrants that falls onto a particular target meadow is determined by two factors: the “attractiveness” of the target meadow, and the probability that a butterfly survives the flight to the target meadow. The attractiveness again is composed of a “distance preference factor” and a “thinning factor”.

First, we consider the probability of surviving the flight to a given target meadow at distance d . We adopt the most commonly used relationship (e.g., Hanski 1999): $P = \exp(-\alpha d)$ where α is the resistance of the landscape meaning that a high α leads to most butterflies already dying after short travel distances. As can be calculated easily, $1/\alpha$ is the mean dispersal distance, i.e. the mean distance that a butterfly can reach alive.

The landscape resistance α depends on the type of landscape. We distinguish “meadow” with $\alpha_m^{-1}=3\text{km}$, open land with $\alpha_l^{-1}=2\text{km}$, forest with $\alpha_f^{-1}=1\text{km}$ and settlements with $\alpha_s^{-1}=0.5\text{km}$. If more than one landscape type crosses the path of a butterfly the easiest way is to draw a straight

line between source and target patches, determine the distances d_x travelled through each landscape type x with $x \in \{m, l, f, s\}$ and $d_m + d_l + d_f + d_s = d$ and calculate the probability of survival as the product of the probabilities of surviving the passage through each of the four landscape types:

$$P = \prod_{x \in \{m, l, f, s\}} \exp(-\alpha_x d_x) = \exp\left(-\sum_{x \in \{m, l, f, s\}} \alpha_x d_x\right) = \exp(-\bar{\alpha}d) \quad \text{with} \quad \bar{\alpha} = \sum_{x \in \{m, l, f, s\}} d_x \alpha_x / d \quad (1)$$

As eq. (1) indicates, the survival probability can be regarded as dependent on the total distance d that has to be crossed against an average landscape resistance $\bar{\alpha}$. This average landscape resistance is the mean of the α_x weighted by the proportion d_x/d of the dispersal path that falls into landscape type x .

This interpretation of eq. (1) allows for a moderation in the unrealistic assumption that the butterflies follow precisely a straight line. Instead we assume that they may deviate to a certain extent to the right or the left and move within a strip 200m wide. The average landscape resistance $\bar{\alpha}$ and the survival probability of a butterfly dispersing from one end of the strip to the other then is calculated by eq. (1), with d_x/d now being the proportion (relative number of pixels) of landscape type x within the strip.

Now we turn to the attractiveness factor and assume for the moment that there is no dispersal mortality to the butterflies. To calculate the attractiveness factor we assume that butterflies prefer closer meadows to meadows further away. We assume that the preference for a certain meadow decreases with the distance d_{ij} between source meadow i and target meadow j via $(\bar{\alpha}_{ij} d_{ij})^{-1}$ where $\bar{\alpha}_{ij}$ is the above defined average landscape resistance between meadow i and j . This means that, e.g., a meadow twice as far away as another has half the attractiveness. Similarly a target meadow which is separated by landscape with higher resistance (e.g., settlement) has accordingly lower attractiveness than a target meadow separated by landscape with lower resistance (e.g., open land).

Even if closer meadows were not preferred, meadows further away would receive fewer butterflies than meadows closer to the source due to the thinning factor. This indicates that a

meadow farther away covers a smaller angle than a closer meadow and just statistically receives fewer butterflies. Precisely, viewed from the source patch, the arc spanned by a target patch diminishes with d_{ij}^{-1} . Altogether, the attractiveness of a target meadow, composed of distance preference and thinning factor, decreases with increasing distance or landscape resistance as $\bar{\alpha}_{ij}^{-1} d_{ij}^{-2}$. As no dispersal mortality is assumed, all butterflies must reach some meadow, so the sum $S_i = \sum_j \bar{\alpha}_{ij}^{-1} d_{ij}^{-2}$ (where $j=1 \dots \text{number of patches, and } j \neq i$) must be one. Thus the factor $\bar{\alpha}_{ij}^{-1} d_{ij}^{-2}$ has to be normalised by dividing it by S_i and the attractiveness of a target patch j for butterflies emigrating from a source patch i becomes $\bar{\alpha}_{ij}^{-1} d_{ij}^{-2} / S_i$.

There is one underlying assumption regarding the attractiveness that needs to be mentioned: The attractiveness does not depend on the quality and current condition of the target meadow. An attractiveness model that relaxes this assumption would complicate the model analysis substantially.

Now we moderate the above assumption of zero dispersal mortality and combine dispersal mortality and attractiveness factor by multiplying them. The total share of emigrants from a source meadow i that reaches a particular target meadow j then is

$$\Phi_{ij} = \frac{\exp(-\bar{\alpha}_{ij} \bar{d}_{ij})}{\bar{\alpha}_{ij} \bar{d}_{ij}^2} \sum_j \bar{\alpha}_{ij} \bar{d}_{ij}^2 \quad (2)$$

with $\bar{\alpha}_{ij}$ being determined by eq. (1).

4.3 Model analysis

The objective of the following analysis is to understand the behaviour of the ecological model without referring to the economic part of the study. To recall, the economic model determines which meadows adopt the promoted mowing regime and, together with the landscape data, how many of such meadows with promoted mowing regimes are in the landscape, what their total area is, where they are located, and what their individual areas are. Ignoring the economic part

therefore essentially means ignoring all the information about the spatial structure of the landscape.

Instead, in this part of the analysis we consider a simple and fictitious landscape in which all patches have equal size, and the distances between all possible pairs of patches are identical. Although such a configuration is physically impossible to achieve in a 2-dimensional landscape, it is nevertheless used frequently in ecological research as a reference model or starting point for more complex research questions like the effects of habitat loss on the survival of species (e.g., Tilman et al. 1994). In the present study, the objective of such an analysis is to gain a general understanding of the effects of the 112 mowing regimes on the viability of a population inhabiting an ensemble of meadows.

In the present context a suitable indicator for metapopulation viability is the total meadow area occupied by the butterfly after a certain number of model years. As the dynamics of the species are stochastic, it is appropriate to use the expected area of meadow occupied. However, the expected value does not include any information about the degree of stochastic variation. Therefore, an alternative measure could be the probability that at least a certain meadow area is occupied (analogue to the so-called quasi-extinction risk concept by Ginzburg et al. 1982). We considered both measures and found that they are very strongly and positively correlated, so below we use only the former, as it is easier to handle.

A landscape of 40 meadows, each of 1 ha size is considered. On each meadow either the conventional or the promoted mowed regime is applied. To make the analysis comparable to the analysis of the ecological-economic model (described in the next section) we consider that, due to the different costs, some promoted mowing regimes can be implemented on larger proportions of the total meadow area than others. The distance between the 40 meadows is set such that the probability to survive the flight from one patch to the other is 0.5 for all pairs of meadows and all meadows have the same attractivity. For all 112 possible mowing regimes the proportion of the 40 meadows that are occupied after 20 years (this proportion is henceforth referred to as

“occupancy”) is recorded. Each simulation is repeated 100 times to account for the stochasticity in the ecological dynamics and an average occupancy is determined.

4.4 Model results

Figure 3 shows the occupancy of the meadows as a function of the applied mowing regime. Eggs and larvae are especially abundant on the plants in the weeks 6 to 9. Thus, mowing in these weeks is very detrimental irrespective of the mowing frequency which is indicated by the black colour in Fig. 3 for these weeks. Furthermore in mowing scenarios with two cuts, mowing in earlier weeks is detrimental, too, if the second cut falls into the weeks of high larvae abundance and thus causes severe larvae mortality. Therefore, the occupancy of scenarios with two cuts is very sensitive both to the time of first mowing and the time between the cuts. The highest occupancy (white colour) is achieved by mowing once per year or every second year either early or late in the season. In these mowing regimes the mowing frequency is high enough to ensure sufficiently high plant and ant nest abundance and at the same time larvae mortality due to mowing is sufficiently low. These results are very robust against variations in the dispersal survival (a range of 0.1...0.9 was tested) and the total number of meadows, as long as the latter was larger than about 40.

An interesting observation is that the occupancy is very sensitive to the applied mowing regime and ranges from zero (for the worst) to one (for the best mowing regimes). In comparison, the proportion of meadow area with promoted mowing regime varies much less (only by a factor of about 2) from the cheapest to the most expensive mowing regimes (Fig. 2b). This indicates that the cost-effectiveness of a promoted mowing regime depends more on its ecological suitability than the proportion of meadow area on which it is applied (i.e., on the cost structure).

5. The ecological-economic model: determining the cost-effective mowing regime

We now turn to the full ecological-economic model to identify the cost-effective mowing regime, i.e. the mowing regime that achieves the highest ecological benefit for a given conservation budget. The analysis considers the ecological and the economic model components as well as the structure of the landscape with the different sizes and locations of the meadows.

The optimisation is carried out for 20 different budget sizes. In order to have a higher resolution at low budget sizes we increase the budgets in a quadratic manner as $B=1000n^2\text{€}$ where $n=1\dots 20$. For each budget B we determine which meadows adopt the promoted mowing regime. On the resulting landscape the butterfly population dynamics are simulated for 20 years and the final total meadow area containing butterflies is recorded. To account for the randomness in the incentive component u of the costs and the randomness in the butterfly population dynamics, the whole analysis is repeated 100 times for each budget and an average, the expected meadow area occupied by butterflies, is taken.

For each budget level, the expected area of meadow occupied is determined for all 112 promoted mowing regimes. Comparison of the results allows the most cost-effective mowing regime(s) to be identified for each budget.

Figure 4 shows the cost-effectiveness of all promoted mowing regimes for various budgets. Mowing regimes that are cost-effective at one budget level are also cost-effective at other budget levels. The compensation payments for the cost-effective mowing regimes as functions of various budgets are shown in Fig. 5. Payments increase with the budget, are positively related to the costs of the mowing regimes and inversely to the meadow area managed according to the promoted mowing regime (Fig. 2).

It is of interest now to compare the results of the full ecological-economic model with those of the ecological model. The comparison of Figs. 3 and 4 reveals that the meadow area occupied by butterflies as obtained from the ecological-economic model and the occupancy as obtained from the ecological model are strongly related in that if a mowing regime leads to a relatively high occupancy in the latter it also leads to a high occupied area in the former. Furthermore, it is plausible that for a given mowing regime the meadow area occupied by butterflies is positively related to the meadow area adopting the promoted mowing regime. This motivates the hypothesis that

the meadow area occupied by butterflies (full ecological economic model: Fig 4) is the product of (a) the meadow area adopting the promoted mowing regime (economic model component: Fig 2b) and (b) the occupancy (obtained from the ecological model in the fictitious landscape: Fig 3).

To test this hypothesis, in Figure 6 the area of occupied meadow as obtained from the ecological-economic model is plotted against the product of promoted meadow area and occupancy, each dot representing one of the 112 mowing regimes. The dots are aligned quite well along the diagonal although there is some scatter which indicates that in some cases a mowing regime that is better than another in the full model may perform worse in the product model. For all budgets, the relative error between the two models is generally largest for the mowing regimes located close to the origin, i.e. those with low performance. Furthermore, the error is largest if the budget is low (4000€). Obviously, in these cases the product model which does not consider the effect of spatial structure on the population dynamics, fails.

This conclusion is reinforced if we recall that the analysis of the performances of the mowing regimes was based on a statistical average, taken over random replicates of the incentive component u . Each random replicate of u leads to a different spatial configuration of meadows adopting the mowing regime and by taking an average we have automatically reduced the impact of spatial configuration on the results. To check the above hypothesis in a stricter manner we also plotted the areas obtained by the full model and the product model not only for the average performances of the 112 mowing regimes but also for their performances obtained for each replicate of u . We found that the variation in the scatter plot somewhat increases, but the general trend remains, such that the product and the full model produce similar results for mowing regimes with high performances (sufficiently large budget and cost-effectiveness) and different results in the other cases.

Following the dominant approach for compensation payments for conservation measures in Europe we assumed that every farmer in the region receives the same payment. However, the question arises how well such an approach performs in comparison to a spatially heterogeneous

policy. Such a policy may lead to a more cost-effective solution because (a) the spatial configuration of promoted meadows affects the survival probability of the butterfly population and (b) the agency can compensate each farmer for his or her individual costs rather than paying all farmers the same amount of compensation.

Although a detailed analysis of option (a) is beyond the scope of this paper we are able to provide a conservative estimate on how much a policy that takes into account the spatial configuration of conservation measures leads to higher cost-effectiveness. As described in Section 3.2, we sampled and evaluated several landscape configurations in order to capture the randomness of u . Comparing the performances of the mowing regime over these landscape configurations provides an estimate on how much the spatial optimisation of the location of promoted meadows would at least increase the performance of the mowing regime. Figure 7a shows the result for one of the most cost-effective mowing regimes, “mowing in the third week of May and four weeks later” (1,-1,4). For small budgets below €10,000 the coefficient of variation of the performances is about 0.25. As plus/minus two coefficients of variation roughly mark the bounds of a 95% confidence interval, this means that good spatial configurations perform at least 50% better than average configurations. With an increasing budget the coefficient of variation decreases indicating that spatial optimisation of meadows becomes less important.

The analysis of option (b) is straightforward. Knowing the budget B_u for spatially uniform payments as a function of the area A of meadows occupied by butterflies, the budget B_h for spatially heterogeneous payments is the derivative of B_u with respect to A times A : $B_h(A) = A dB_u / dA$. Figure 7b shows how much money ($B_u - B_h$) could be saved with heterogeneous payments. For budgets below ca. €30,000 the saved amount increases with increasing variation in the farmers' attitudes towards conservation. This is because increasing variation decreases the costs of the cheaper meadows where conservation measures are carried out for small budgets. For budgets above €30,000 the opposite is found and increasing variation in farmers' attitudes

decreases the amount of money ($B_u - B_h$) saved. Except for very small budgets and low variation in farmers' attitudes, the amount saved by spatial differentiation of payments is quite substantial.

6. Discussion

The aim of this paper is to advance the research on the cost-effectiveness of compensation payments in four areas (cf. Introduction). We will discuss each area separately:

(1) A model-based approach for designing cost-effective payments in real landscapes

Using the example of the conservation of a butterfly species protected by the EU Habitats Directive, a model-based approach is presented which is able to develop cost-effective compensation payment schemes for conserving endangered species in real landscapes. Although the results from our case study are specific to the area and species studied, the methodology is general and applicable elsewhere. The landscape data are obtained from the GIS analysis of a satellite image. An *economic model* determines the costs of different conservation measures. In the example presented here, the costs of various mowing regimes are calculated through the method of standard gross margin calculations. The costs, together with the available budget, determine the spatial structure and temporal dynamics of the landscape. An *ecological model* simulates the population dynamics of the species in the landscape and determines the effect of various conservation measures on the population. In the example, we calculate the effect of different mowing regimes on the (expected) meadow area occupied by butterflies after 20 model years. As a result, for a given budget the ecological benefit is known for each conservation measure which allows identification of the most cost-effective one(s) and the corresponding compensation payment(s).

(2) Analysing the influence of metapopulation dynamics

To understand the relative contributions of economic and ecological parameters in our example, the population dynamics are studied also in a fictitious landscape. Here, the locations of the meadows are not considered explicitly. We find that the cost-effectiveness of a mowing regime is more determined by its ecological suitability than by its cost. In first approximation we also find

that the meadow area occupied by butterflies in the real landscape is the product of the meadow area adopting the promoted mowing regime and the occupancy (proportion of area occupied by butterflies under this mowing regime) as determined from the simplified ecological model. This result stems mainly from the limited importance of spatial configuration, such that the location where a particular mowing regime is applied does not significantly affect the survival of the butterfly. The simple picture, however, changes when the budget is small and the cost-effectiveness of the mowing regime is low, such that altogether the area of occupied meadows becomes small. Then the product model does not well approximate the ecological-economic model, indicating that the spatial location of meadows matters (Fig. 7a). This result can be explained with the ecology of metapopulations.

Metapopulations are composed of subpopulations, each inhabiting individual meadows and interacting via the exchange of individuals. Metapopulation dynamics are governed by three central processes: the extinction of subpopulations, the re-colonisation of empty habitats, and the stabilisation of subpopulations through immigrants from neighbouring populations (Hanski 1999). As the cost-effectiveness of a mowing regime is mainly determined by its ecological suitability, there is a strong correlation between the cost-effectiveness of a mowing regime and the stability of the local populations. Depending on budget and choice of mowing regime we may, therefore, be confronted with very different types of butterfly metapopulation dynamics (Fig. 8).

If the cost-effectiveness of the promoted mowing regime is very low, the local populations on the individual meadows are critically unstable irrespective of the available budget. Even the interaction of different local populations cannot prevent the metapopulation from rapid extinction (Drechsler and Wissel 1998). Spatial configuration has no influence.

Now consider slightly more cost-effective mowing regimes. Here the local populations are still unstable and cannot persist in isolation. However, if the meadows with promoted mowing regimes are close enough to each other, there is sufficient exchange of individuals between meadows and the species can survive as a metapopulation. For small budgets only few meadows with the

promoted mowing regime exist in the landscape, and it is important to have these meadows arranged together in one part of the landscape: spatial configuration matters. For high budgets there are so many meadows with the promoted mowing regime that even under random allocation the distances between neighbouring meadows are so small that butterflies can disperse between them. Metapopulation dynamics exist regardless of the spatial configuration of meadows. In between these two extremes the importance of spatial configuration increases with decreasing budget.

Now consider the most cost-effective mowing regimes. Such mowing regimes lead to relatively stable local populations which are less reliant on immigrating butterflies. Therefore, the species can survive as a metapopulation even if the meadows are further apart than would be optimal. Spatial configuration still matters, but it matters less than in the above case of less cost-effective mowing regimes with unstable local populations (Groeneveld 2004).

Combining all these findings (and excluding the mowing regimes that lead to critically unstable local populations), we conclude that the importance of spatial configuration increases with decreasing budget – more strongly if the promoted mowing regime is less cost-effective and less strongly if the promoted mowing regime is more cost-effective. We observe that an economic parameter – the budget – governs via the ecology of metapopulations the importance of spatial configuration of meadows (implications for instrument design are outlined below). This result demonstrates that integrating metapopulation dynamics in the analysis of spatial issues in economic biodiversity research is essential and more research is required to better understand its effects from an economic point of view.

(3) Spatial heterogeneity of compensation payments

Research has emphasised that spatially differentiated benefit functions (a) and cost functions (b) call for spatially heterogeneous policy instruments. Our case study contributes to this mostly theoretical research with empirical results.

(a) Conceptual models have shown that for spatially differentiated benefit functions the criterion of cost-effectiveness requires spatially heterogeneous conservation measures and compensation payments (e.g. Babcock et al. 1997, Wu and Bogess 1999, Wätzold and Drechsler 2005). The case study result shows that well-designed spatial configurations of the meadows with promoted mowing regimes may lead to ecological benefits which are 50% higher than benefits from average configurations (Fig. 7a). This result suggests that the issue of spatial heterogeneity of conservation policies may be of significant practical importance.

The case study draws attention to two aspects that have not been addressed in the above mentioned conceptual research. First, metapopulation dynamics which leads to spatial heterogeneity of the benefit functions in this case study, has been neglected. Second, designing cost-effective heterogeneous payments may prove difficult for some conservation problems. The reason is that the (added) benefit of a meadow - and so the cost-effective compensation payment for that meadow - depends on the presence and the locations of other meadows with promoted mowing regimes in the region which are not known a priori to the regulator. Higher marginal benefits of a meadow with the promoted mowing regime only arise if the meadow is closely located to other meadows with the promoted mowing regime. To initiate such agglomeration one possible option for the agency may be to randomly choose a particular area where payments are higher. However, there is a risk that an area is selected where costs are comparatively high, for example due to a negative attitude of farmers towards conservation (cf. Smith and Shogren 2002). Furthermore, it may be perceived as unfair by farmers if there is an arbitrary differentiation of payments. An alternative to such a differentiation of compensation payments may be an agglomeration bonus (Parkhurst et al. 2002) where a bonus is paid on top of a compensation payment when the meadow to be mowed for conservation is close to an area where other conservation measures are carried out. It is a matter of further research to analyse to what extent and under what circumstances an agglomeration bonus provides a better solution than spatially differentiated payments.

(b) Several authors emphasised that uniform compensation payments lead to producer surpluses if conservation costs differ among land users (e.g. Innes 2000, Smith and Shogren 2002). If producer surpluses exist, a higher financial budget for achieving a given conservation aim is required compared to an identical situation where payments are differentiated based on true costs. A higher budget, in turn, leads to a welfare loss as the taxation required to finance public funds has a distortionary effect on consumption and/or production. In the present study, we found (Fig. 7b) that depending on the variation in the farmers' attitude towards conservation and the budget the production surplus may be substantial. Payments differentiated according to individual farmers' costs may require up to only half the budget than homogeneous payments. This result demonstrates the importance of cost-based differentiation as for similar situations (farming in Europe) we may find even higher savings. In our study costs only differ due to meadow size and the different attitudes of farmers towards conservation whereas in other circumstances costs may additionally differ according to the other variables considered in the economic model (soil quality, soil humidity, altitude). This calls for an increasing consideration of payment schemes that aim to reduce producer surpluses such as auctions (Latacz-Lohmann and van der Hamsvoort 1997) or payments that are negotiated with individual farmers (Whitby and Saunders 1996).

(4) Evaluation of existing payment scheme

The case study allows analysing a payment scheme that already exists in the region of Landau. Farmers may participate in a programme where they receive a compensation of 200 € per ha when they commit themselves not to mow before 15 June. Similar schemes exist all over Germany and in many other parts of Europe. Their aim is to improve the conservation of meadows in general and of meadow birds in particular. With this restriction on the mowing date, it is profit maximising for farmers if the first mowing is in the third week of June (coded as (1,3,6) in this paper). As Fig. 4 shows, such a mowing regime is ranked very low in terms of cost-effective conservation of *M. teleius*. In fact, it has a negative impact on the *Maculinea* population, as here the second mowing falls into the critical phase where the butterflies deposit their eggs on the *Sanguisorba* plants. While a

criticism of the existing scheme has to take into account that it is not explicitly focused on *M. teleius*, our analysis demonstrates that the existing scheme fails to cover all relevant ecological objectives. *M. teleius* is protected by the EU Habitats Directive and, therefore, has a high priority for conservation in Europe. This criticism is all the more important as schemes similar to the programme in Landau exist all over Germany, whereas to our knowledge no programme is specifically directed at *M. teleius*. There are no studies that analyse the reasons for this uniformity of conservation programmes across Germany. Anecdotal evidence suggests that conservation programmes that are implemented in one region are just copied in other regions. Scientific research like this study can be used to demonstrate that a spatially heterogeneous approach is better in terms of conservation and cost-effectiveness than the uniform approach that currently exists in Germany.

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Figure 1: The model landscape (black: settlement/roads; dark grey: forest; light grey: open land, water bodies; white: meadows). The dimension of the map is 10x6 km².



Figure 2: (a) Annual costs of mowing versus week of (first) mowing if mowing takes place every year (lines without circles) or every second year (lines with circles). There may be one mowing in a mowing year (solid lines) or two mowings (dashed lines; here from top to bottom: second mowing takes place 8, 4, 6 weeks after first mowing). (b) The expected meadow area with the promoted mowing regime as a function of the promoted mowing regime for a budget of 64,000€ with $u_0=50\text{€}$. The promoted mowing regime is characterised by the week of first mowing (1 is the first week of June) and the frequency of mowing (here the first number stands for mowing every single (1), or second (2) year; the second number indicates whether in a mowing year there are two cuts, separated by 4, 6, or 8 weeks, or only one cut (0)). Black colour represents an area of 300 ha, white colour an area of 700 ha; grey colours represent intermediate values on a linear scale.

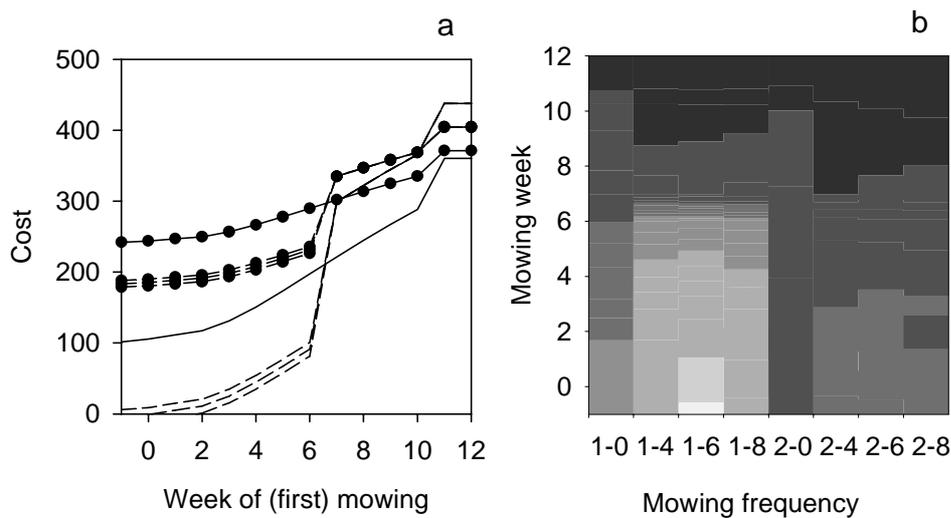


Figure 3: The occupancy as obtained from the ecological model component as a function of the mowing regime. The occupancy is given by the colour on a linear scale where white colour represents a value of one and black colour a value of zero. Other details as in Fig. 2b.

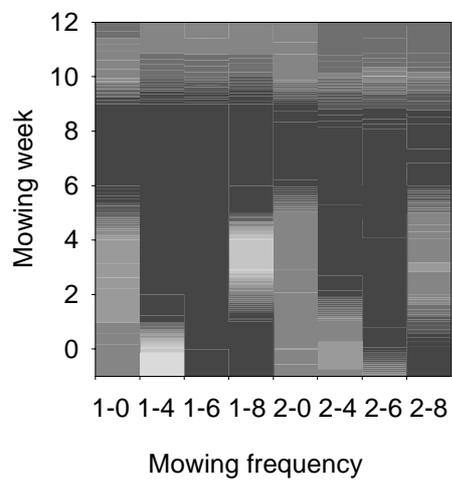


Figure 4: The meadow area occupied by butterflies as a function of the promoted mowing regime. The budget sizes are 4,000€, 16,000€, and 64,000€. The area is given by the colour on a linear scale where black colour represents all meadows being unoccupied and white colour indicates occupied areas of 200ha, 400ha and 700ha, respectively. Other details as in Fig. 2b.

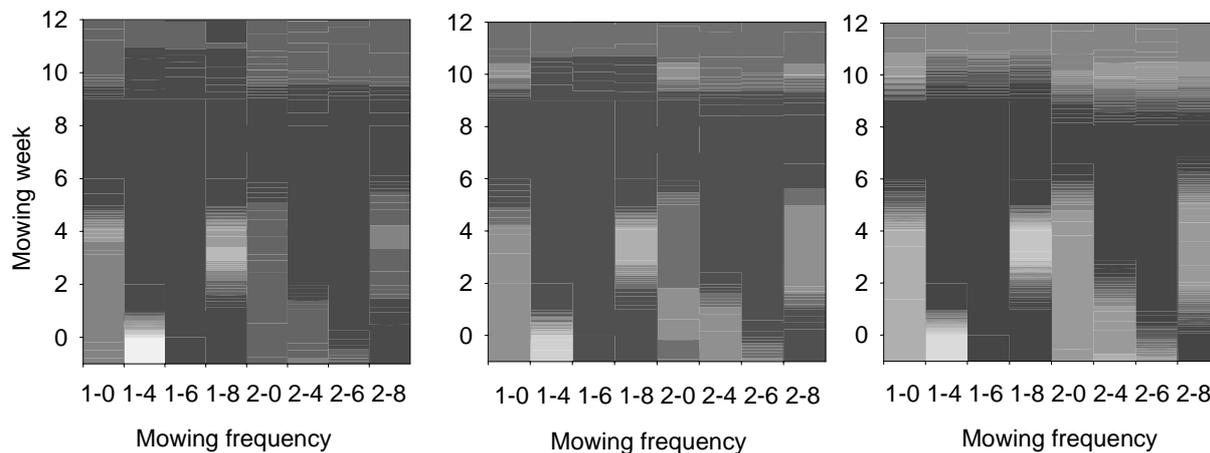


Figure 5: Compensation payments in € as a function of the mowing regime for three budget levels: 4,000€, 16,000€, 64,000€. The payments are given by the colour on a linear scale where black and white colour represent about 50€ and 250€, respectively. Other details as in Fig. 2b.

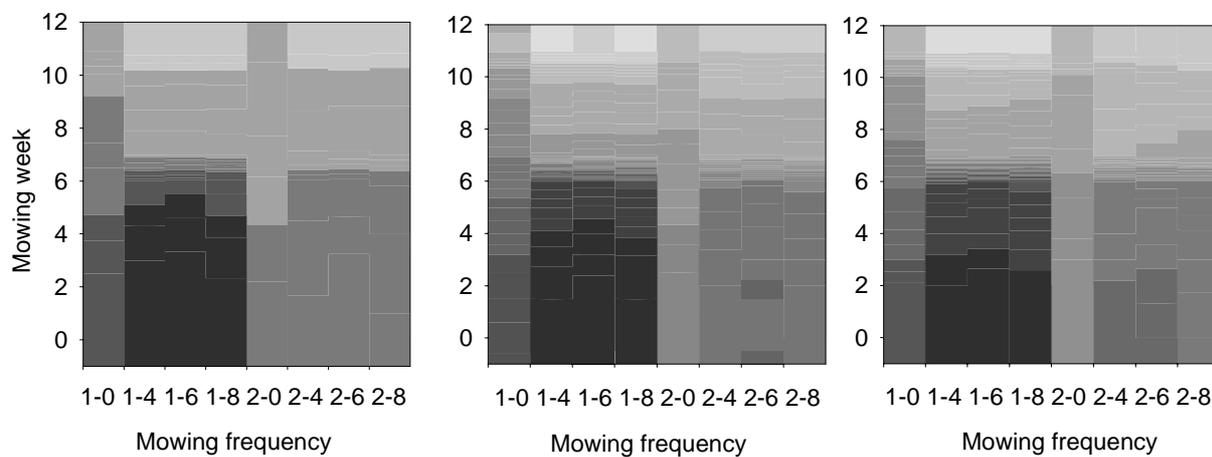


Figure 6: Meadow area occupied by butterflies according to the product model versus area occupied according to the full ecological-economic model (measured in ha). The area in the product model is the product of the area adopting the promoted mowing regime and the occupancy as it is obtained from the ecological model component. Each dot represents one of the 112 different promoted mowing regimes. The budgets are 4,000€, 16,000€, and 64,000€.

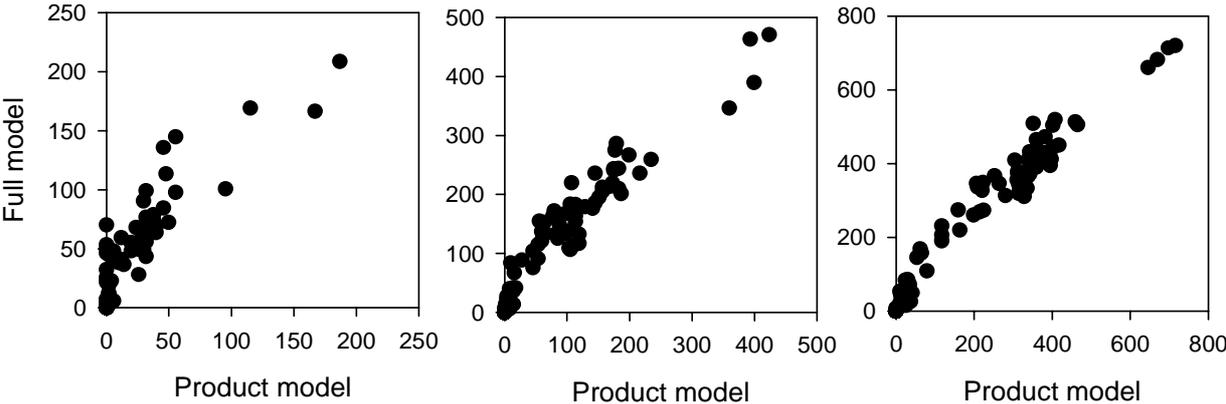


Figure 7: (a) Coefficient of variation of the performance of the mowing regime (1,-1,4) as a function of the budget; (b) Budget required to obtain a particular occupied meadow area for uniform (bold solid line) and heterogeneous payments (thin lines). In the heterogeneous payments the variation of the farmers' attitudes towards conservation is $u \in [-u_0, +u_0]$ with $u_0 = \text{€}50, \text{€}100, \text{€}200$ (solid, dashed, and dotted lines, respectively).

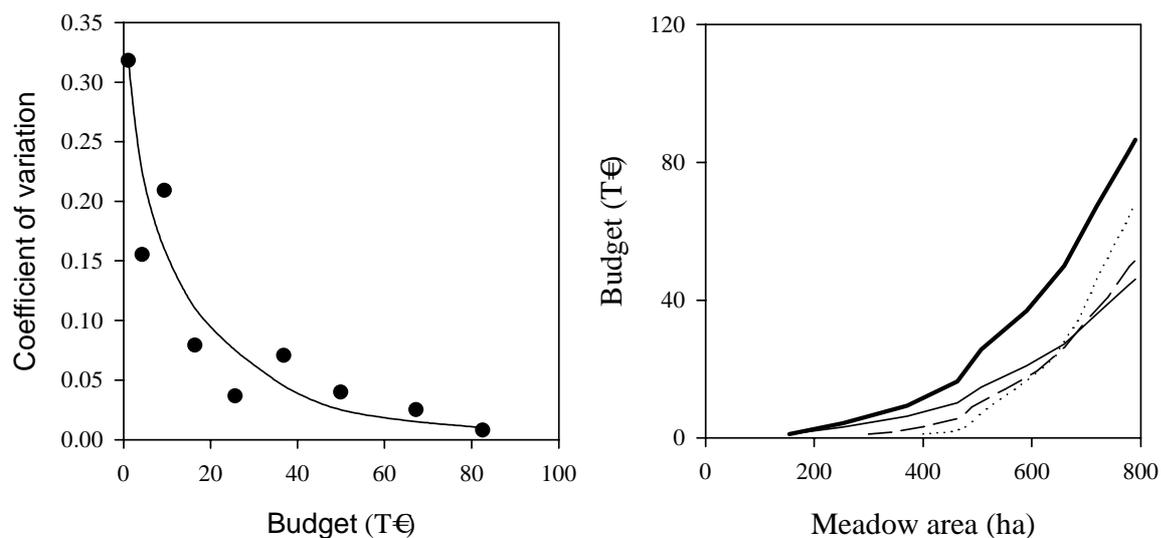


Figure 8: The importance of the spatial configuration of the meadows with promoted mowing regime in dependence of the budget and the cost-effectiveness of the promoted mowing regime. Lighter areas indicate a higher stability of the local populations on individual meadows.

