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**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 compensation payment scheme for conservation of an endangered butterfly species (*Maculinea teleius*) protected by the EU Habitats Directive in the region of Landau, Germany. The economic model determines the costs of relevant conservation measures – mowing meadows at different times and frequencies - and the ecological model quantifies the effects of these mowing regimes on the butterfly population. By comparing the ecological effects of different mowing regimes, the cost-effective regime and the corresponding payments are determined as a function of the conservation budget. The results of the case study are used to analyse the effect of metapopulation dynamics on the cost-effectiveness of compensation payment schemes, to evaluate an existing scheme in the region of Landau and to draw conclusions for the institutional design of payment schemes.

Key words:

Conservation, biodiversity, metapopulation, cost-effectiveness, ecological-economic modelling

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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, Innes 2000). 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), the 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.

With regard to 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. This is being done by developing 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 three respects.

(1) Compared to the research by Johst et al. (2002) the paper aims at developing an approach that is able to determine cost-effective compensation payment schemes for species conservation in real landscapes. This requires the use of a Geographical Information System (GIS) that stores all the relevant landscape data to be integrated into the ecological-economic model. 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 grossmargin calculations.

(2) The *Maculinea* 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). While metapopulations have been thoroughly analysed in ecology, their integration into economic analysis has been largely restricted to issues of optimal exploitation of marine resources (e.g. Sanchirico and Wilen 2001) and optimal harvesting (Bulte and van Kooten 1999). The present case allows for a discussion regarding how the existence of metapopulation dynamics affects the cost-effective design of compensation payments for biodiversity-enhancing land-use measures. To our knowledge this has been done only by Groeneveld (2004). The present model study goes beyond Groeneveld in that (1) different compensation payment schemes (inducing different measures) are compared with regard to their cost-effectiveness and (2) the effect of a change in the conservation budget is analysed explicitly.

(3) The results of the case study are used to contribute to various discussions related to compensation payments for biodiversity-enhancing land-use measures. This includes discussions on the spatial differentiation of compensation payments, on their institutional design, and -as a payment scheme for biodiversity-enhancing land use measures exists in the region of Landau – on the evaluation of existing schemes.

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 steps 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: the real landscape with the spatially and temporally differentiated land use pattern is considered for the identification of 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.

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 $10 \times 6 \text{ km}^2$.



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 $2 \times 4 \times 14 = 112$ 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: Compensation for the foregone profit that arises because the farmer cannot carry out the profit-maximising mowing regime, the farmer’s personal attitude towards conservation, and an “incentive component” to participate in the payment scheme of 100€ per ha. Such incentive components are common practice in EU agricultural schemes.

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.

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 a strong aversion to the conservation programme, irrespective of financial compensation (cf. Smith and Shogren 2002). We assume that for each meadow u is a uniform random variable with $u \in [-50\text{€}, +50\text{€}]$. Even though several meadows may belong to the same farmer, the legal obligation to observe confidentiality restricts access to such information and we have to assume that the u are uncorrelated among the meadows.

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.

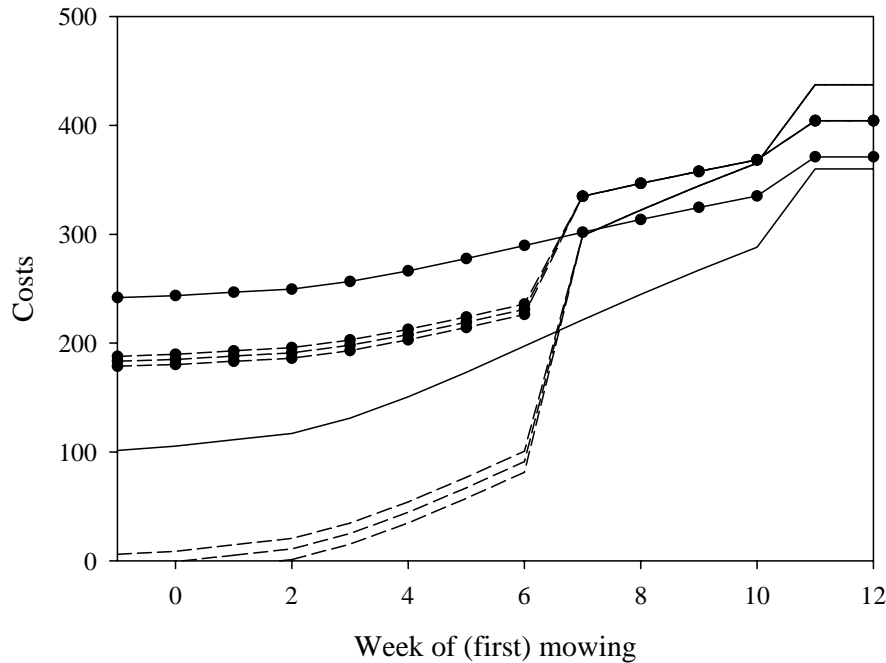
To determine p for a given budget B (the amount of money that can be spend on conservation in the region of interest) we start with $p = 1 \text{ €/ha}$ and successively increase the payment in steps of 1 €/ha . In each step we determine which meadows adopt the promoted mowing regime and determine how 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 2 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.

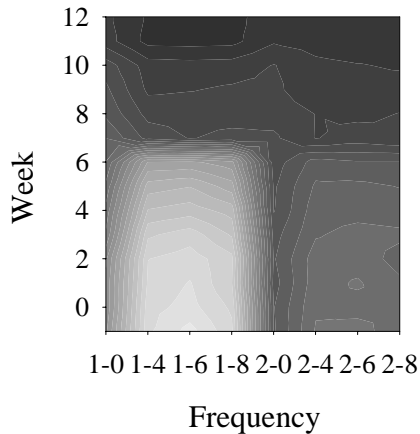
Figure 2: Annual costs of mowing versus week of (first) mowing if mowing takes place every year (lines without circles) or every second year (lines with circles). There may be one mowing in a mowing year (solid lines) or two mowings (dashed lines; here from top to bottom: second mowing takes place 8, 4, 6 weeks after first mowing).



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. This area is shown for all 112 mowing regimes and a budget of $B=64,000\text{€}$ in Fig. 4 and will be used in further analyses and discussions.

Figure 3: The expected meadow area adopting the promoted mowing regime as a function of the promoted mowing regime for a budget of 64,000€ 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 mowings, separated by 4, 6, or 8 weeks, or only one mowing (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.



4. Ecological model

4.1 The local dynamics

The local dynamics of the butterfly *M. teleius* on an 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 details of the model used in this study 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, α^{-1} 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:

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

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 $j=1 \dots$ 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 (for instance, Tilman et al. 1994, Bascompte 1996). 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.

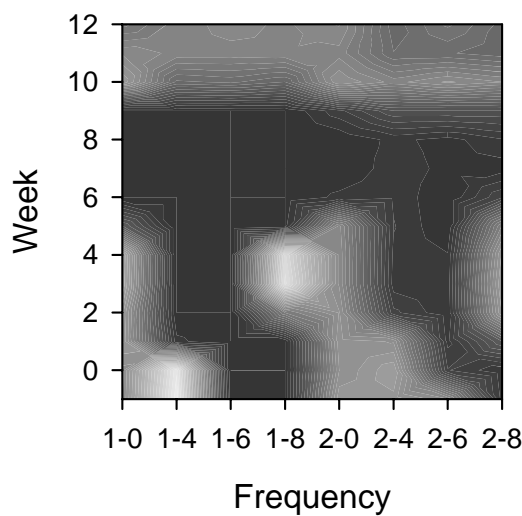
A landscape of 40 meadows, each of 1 ha size is considered. On each meadow either the conventional or the promoted mowed regime is applied. To make the analysis comparable to the analysis of the ecological-economic model (described in the next section) we consider that, due to the different costs, some 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 4 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. 6 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.

Figure 4: The occupancy as obtained from the ecological model component as a function of the mowing regime. For the notations on the axis of the figure, see Fig. 3. 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.



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. 3). 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 in the study region

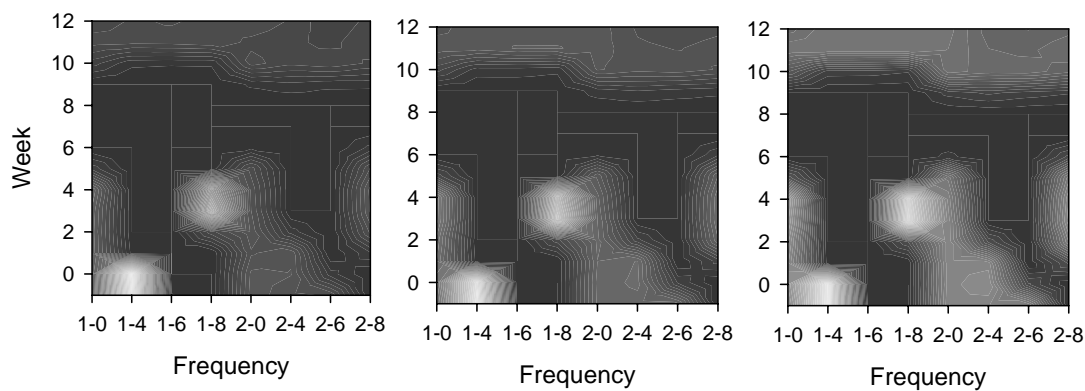
We now turn to the full ecological-economic model to identify the cost-effective mowing regime, i.e. the mowing regime that achieves the highest ecological benefit for a given conservation budget. The analysis considers the ecological and the economic model components as well as the structure of the 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, similar to Section 3 for each budget the whole analysis is repeated 100 times 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.

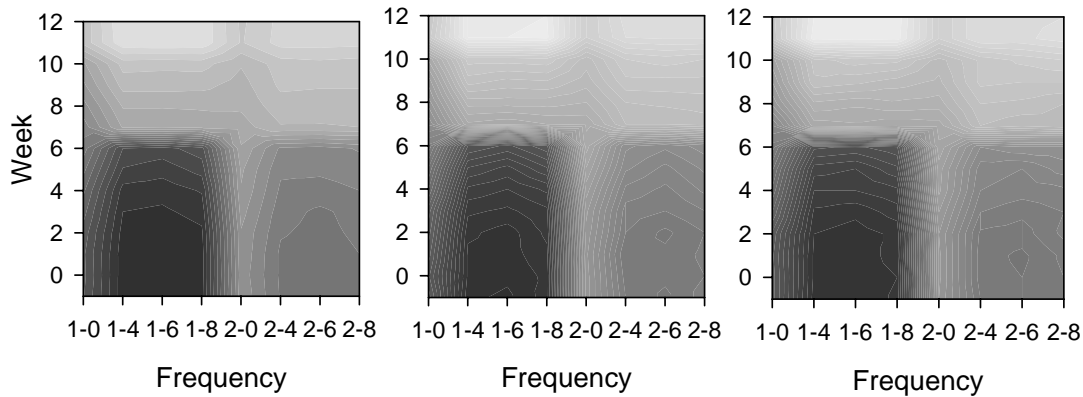
Fig. 5 shows the performances of all promoted mowing regimes for budgets between 4,000€ and 64,000€. The most cost-effective mowing regimes are indicated by white colour. As expected, the larger the budget, the higher the area of meadow occupied. A less expected result is that mowing regimes that are cost-effective at one budget level are also cost-effective at other budget levels, which can be concluded from the observation that in all three panels the white areas are located in the same places.

Figure 5: The meadow area occupied by butterflies as a function of the promoted mowing regime (for details, see Fig. 3). 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.



The compensation payments for the cost-effective mowing regimes as functions of various budgets are shown in Fig. 6. Payments increase with the budget, are positively related to the costs of the mowing regimes (Fig. 2) and inversely to the meadow area managed according to the promoted mowing regime (Fig. 3).

Figure 6: Compensation payments in € as a function of the mowing regime (cf. Fig. 3) 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.

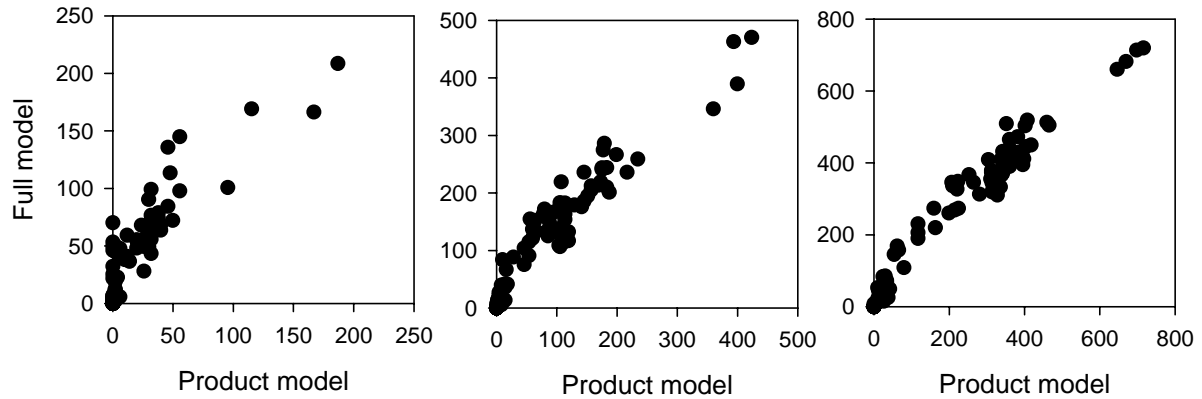


It is of interest now to compare the results of the full ecological-economic model with those of the ecological model. The comparison of Figs. 4 and 5 reveals that the meadow area occupied by butterflies as obtained from the ecological-economic model and the occupancy as obtained from the ecological 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. 5) is the product of (a) the meadow area adopting the promoted mowing regime (economic model component: Fig. 3) and (b) the occupancy (obtained from the ecological model in the fictitious landscape: Fig. 4).

To test this hypothesis, in Figure 7 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.

Figure 7: 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€



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.

6. Discussion

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. An economic model determines the costs of different conservation measures. In the example presented here, these are various mowing regimes that affect the survival of the butterfly. The costs, together with the available budget, determine the spatial structure and temporal dynamics of the landscape. An ecological model simulates the butterfly population dynamics in this landscape and determines the effect of the mowing regimes on the population, particularly 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 mowing regime which

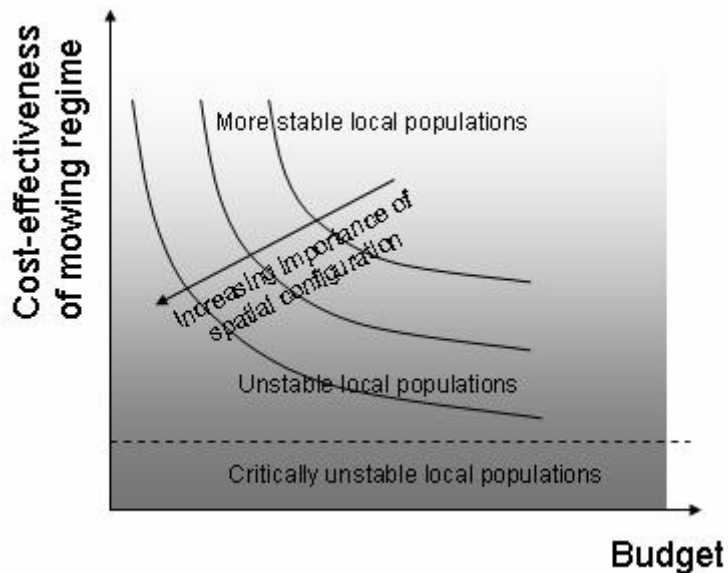
allows identification of the most cost-effective one(s) and the corresponding compensation payment(s).

To delineate the relative contributions of economic and ecological parameters, the population dynamics are not only studied in the real landscape but also in a fictitious landscape in which the locations of the meadows are not considered explicitly. In first approximation we 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. We further find that the cost-effectiveness of a mowing regime is more determined by its ecological suitability for the butterfly than by its cost.

The simple behaviour where the ecological-economic model output decomposes into an ecological quality factor (determined from an analysis where space is only considered in a simple and implicit manner) and an economic quantity factor (total area of suitable meadows) is mainly a result of 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 does matter.

The reason for this can be found in 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 promoted 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).

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.



If the cost-effectiveness of the promoted mowing regime is very low, the local populations on the individual meadows are critically unstable. Even the interaction of different local populations cannot prevent the metapopulation from rapid extinction (Drechsler and Wissel 1998). Spatial configuration has, of course, 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 regime are close enough to each other, there is sufficient exchange of individuals between meadows and the species can survive as a metapopulation. If the budget is very small, only few meadows with the promoted mowing regime exist in the landscape, and it is important to have these all arranged together in one part of the landscape: spatial configuration matters. This changes as the budget increases. At very high budgets there are so many meadows with the promoted mowing regime in the landscape, that even under random allocation the distances between neighbouring meadows would be so small that butterflies could disperse between them. Metapopulation dynamics exist regardless of the spatial configuration. In between these two extremes the importance of spatial configuration increases with decreasing budget.

Now consider more cost-effective mowing regimes. Such mowing regimes lead to more 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 this findings (and excluding those cost-ineffective mowing regimes that lead to critically unstable local populations), one can conclude that the importance of spatial configuration increases with a decreasing budget, and it does so more strongly if the promoted mowing regime is less cost-effective and less strongly if the promoted mowing regime is more cost-effective.

To assess the general consequences of these results on the design of instruments for biodiversity conservation, it is worthwhile to discuss them in the light of conceptual models that address the issue of cost-effective spatial allocation of conservation measures and payments (e.g. Babcock et al. 1996, Wu and Bogess 1999, Wätzold and Drechsler 2005). The research closest to the case study presented in this paper is Wätzold and Drechsler (2005) who compare the cost-effectiveness of spatially homogeneous and heterogeneous compensation payments in a model with two regions that differ in their cost and benefit functions. For higher budgets and more cost-effective mowing regimes in the case study, it does not matter where an additional meadow is included in the programme; this corresponds to a situation in Wätzold and Drechsler with constant marginal benefits in both regions where spatially homogeneous compensation payments – the chosen approach in the case study - provide a cost-effective solution. For low budgets and less cost-effective mowing regimes (cf. Fig. 8) the benefits of an additional meadow differ depending on its specific location, which corresponds to a situation in the conceptual model with constant marginal costs and different marginal benefits in both regions where cost-effectiveness requires spatially heterogeneous payments. However, designing cost-effective heterogeneous payments may prove difficult in the context of the case study. 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 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 it pays a higher compensation. However, there is a risk that an area is selected where costs are comparatively high 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. To what extent such an agglomeration bonus provides a better solution in terms of cost-effectiveness is a matter for further research.

Several authors have expressed concern 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. While this welfare loss provides an argument for tailoring payments according to each farmer's conservation costs, the regulator may encounter significant transaction costs to gain the relevant information about such costs. Whitby and Saunders (1996) explicitly address this trade-off between the transaction costs required to identify the lowest possible compensation payments for each farmer and farmers' producer surpluses that arise through uniform payments in a case study with two payment schemes in England. In Environmentally Sensitive Areas (ESAs) an equal amount of compensation is paid to all land-users for a package of prescribed conservation management practices, whereas for management agreements on Sites of Specific Scientific Interest (SSSI), payments are negotiated with individual land-users based on their costs for conservation measures. On comparing both schemes, they find that the lower transaction costs in the ESAs scheme are not sufficient to offset the higher transfers, and SSSI payments therefore require overall less public expenditure. Although we made no explicit calculations, the case study in this paper seems to provide a counter example because costs only differ due to the different attitudes of farmers towards conservation and meadow size. This implies that producer surpluses, and therefore also possible reductions in public expenditure due to cost differentiation, are rather low and will most likely not offset the higher transaction costs.

The case study also 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 € when they commit themselves not to mow before 15 June (Ministerium für Umwelt und Forsten 2000). Similar schemes exist all over Germany and in many other parts of Europe and

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 to mow in the third week of June (coded as 1-3-6 in this paper). As can be seen in Fig. 5, 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 this scheme has to take into account that the scheme is not explicitly focused on *M. teleius*, our analysis demonstrates that the existing scheme fails to cover all relevant ecological objectives, as *M. teleius* is protected by the EU Habitats Directive and, therefore, has a high priority for European conservation. This criticism is all the more important as similar programmes are applied all over Germany, whereas to our knowledge no programme specifically directed at *M. teleius* exists. The general conclusion from this observation is that if conservation measures are focused on specific species, the effects on other species have to be carefully analysed.

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