Biodiversity conservation in a dynamic world may lead to inefficiencies due to lock-in effects and path dependence

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Abstract

Although biodiversity is still diminishing at an alarming rate, in some areas its conservation is expanding. The exact path of this expansion, however, is uncertain. This can lead to problems of path-dependence and lock-in effects. Path dependence describes situations where history strongly influences present decisions and lock-in effects refer to situations where an earlier decision provides strong incentives to follow a particular path, even if more efficient alternatives are available later on. Both concepts have been studied by economists and social scientists in various applications. However, to our knowledge these concepts have not been applied to the analysis of biodiversity conservation policies and strategies in a modelling framework. Here, we develop a conceptual ecological-economic model to investigate which ecological and economic parameters favour the appearance of efficiency losses in biodiversity conservation due to path dependence and lock-in effects in a dynamic two-period two-region model. Generally we find that efficiency losses occur if there are signals that guide the first-period budget into a region that later turns out to be suboptimal if both time periods had been considered right from the beginning. This is, for example, the case if level and slope of marginal costs are small in the region with the less convex ecological benefit function, so that the first-period budget is misguided into the less costly region, ignoring that for larger budgets the ecological benefit is lower than in the other region. To illustrate the conservation relevance of our findings, we present potential efficiency losses through path dependence in the hypothetical case of applying offsets to conserving the endangered *Maculinea teleius* butterfly near the city of Landau in Germany.

Key words: dynamic optimisation, ecological-economic model, ecological benefit, economic cost, efficiency, resource allocation.

Introduction

Global biodiversity is declining at an alarming rate (Butchart et al. 2010). Despite this general negative trend, biodiversity conservation is expanding in some areas. Examples include the enlargement of reserve sites (Morales-Hidalgo et al. 2015), the generation of new habitats through financial means from offsets (Wende et al. 2018), the implementation of conservation easements (Rissmann et al. 2013), and land purchase by conservation agencies and NGOs (Schöttker and Wätzold 2018). This expansion, however, is typically slow and the exact path of expansion is unknown as the future political situation regarding biodiversity conservation (Haila and Henle 2014) and the availability of future conservation budgets (Drechsler and Wätzold 2007) are full of uncertainties. This means that decision makers have to make conservation decisions today without knowing to what extent conservation expansion is possible in the future.

In their analyses of decisions and their consequences in a dynamic and uncertain world, economists and social scientists have identified path dependence and lock-in effects as important factors that affect the long-term consequences of present decisions and may lead to inefficiencies (David 1985, North 1991). The concept of path dependence typically is used to describe situations where history, i.e. previous conditions, strongly influences present decisions (Liebowitz and Margolis 1995). The term lock-in has been used to explain that an earlier decision provides strong incentives to follow a particular path – to be locked-in in that path - even if more efficient alternatives are available later on (David 1985). Applications of the concepts of path dependence and lock-in effects are found in the fields of technology development (Ruttan 1997), organisational analysis (Sydow et al. 2009), and institutional change (North 1991), among others.

There are also some studies that use these concepts in environmentally related research. Barnett et al. (2015) investigate how the path-dependent nature of the institutions limit today's climate change adaptation in Australia. Unruh and Carrillo-Hermosilla (2006) argue that due to industrial lock-in effects developing countries are unlikely to leapfrog carbon intensive energy production, and regarding agricultural land use, Sutherland et al. (2012) use path dependence to explain farmers' resistance to move towards environmentally beneficial land use. The closest analysis to biodiversity conservation that we found is the application of the concept of path dependence to explain the emergence of payments for ecosystem services (Bidaud et al. 2013). However, to our knowledge, there is no further research that applies the concept of path dependence and lock-in effects in a systematic manner to biodiversity conservation policies and strategies.

This is somewhat surprising as there is quite a lot of literature about biodiversity conservation in a dynamic and uncertain world (Costello and Polasky 2004, Meir et al. 2004, Pressey et al. 2007). For example, Johst et al. (2011) and Van Teeffelen et al. (2012) discuss the impact of habitat network dynamics on species conservation. Adopting a more historical perspective Dallimer et al. (2009) address land use change, habitat change, and how stakeholders perceive it in the Peak District in England. Other research addresses the risk of land-use conversion (Strange et al. 2006), the impact of price uncertainty on different aspects of agri-environment policies (Barraquand and Martinet 2011), and how to optimally allocate conservation budgets over time, considering budget uncertainty (Drechsler and Wätzold 2007) and flexibility (Lennox et al. 2017). Final examples are analyses on the impact of land market feedbacks on reserve selection (Butsic et al. 2013), the impact of policy adjustment costs on species management if ecosystems change (Boettiger et al. (2016), the cost-effective mitigation of threats to biodiversity conservation (Auerbach et al. (2015), and the combination of threat mitigation with different types of discounting (Armsworth 2018).

The overall purpose of this paper is to contribute to the application of the concepts of path dependence and lock-in effects to the analysis of biodiversity conservation in a dynamic and uncertain world. Our research is novel as, to our knowledge, we present the first paper that applies a modelling approach to analyse path dependence and lock-in effects in biodiversity conservation. More specifically, we develop a conceptual ecological-economic model to identify ecological and economic parameters which might favour efficiency losses due to path dependence and lock-in effects in the context of the efficient spatial allocation of conservation measures.

For our analysis, we develop a model with two regions and two time periods, and compare two settings. In a 'myopic setting', the conservation agency only knows before each period the budget for that period and has no information about the budget in the second period. In an 'optimal setting', the agency is informed in the beginning about the budgets available in both periods. In comparison with the optimal setting, efficiency losses may occur in the myopic setting due to path dependence and lock-in, such that the agency invests the budget in a region where it turns out to be sub-optimal in hindsight. We analyse which characteristics of economic and ecological parameters favour such efficiency losses. To demonstrate the practical relevance of our findings, we present potential efficiency losses through path dependence and lock-in in the hypothetical case of applying payments financed by offsets to conserve the Large Blue butterfly, *Maculinea teleius*, in a region near the city of Landau in Germany.

2. Methods

2.1 The model

We consider two regions that differ by their ecological benefit functions, their economic cost functions and their initial habitat area. For the choice of the benefit functions we build two scenarios:

(a) the benefit functions are concave or convex to varying degrees, such that the benefit B_i in region i (i = 1,2) is given by:

$$B_i = A_i^{z_i} \tag{1a}$$

where A_i is the habitat area in region i and z_i a region-specific constant.

Concave benefit functions ($z_i < 1$) may be motivated by the species-area relationship that tells that the number of species in a region increases with the size of that region in a concave manner (Begon et al. 1990, Table 22.1), or by the fact that the expected life time of a population subject to strong environmental fluctuations increases less than linearly with increasing habitat area (Lande 1993, Wissel et al. 1994). Convex benefit functions ($z_i > 1$) may arise due to threshold effects or the fact that the expected life time of a population subject to weak environmental fluctuations increases more than linearly with increasing habitat area ((Lande 1993, Wissel et al. 1994). In the case study in section 4 we will use that (in the absence of spatial environmental correlations) the viability of a metapopulation increases with increasing number of habitat patches in a convex manner. Examples of concave and convex benefit functions are shown in Fig. 1a.

(b) the benefit functions are saturating, such that the benefit is given by

$$B_i = \frac{A_i^{z_i}}{A_i^{z_i} + k_i} \tag{1b}$$

where k_i and z_i are constants. In a saturating benefit function the benefit is limited to some maximum value, which in the present formulation is equal to one. For $z_i > 1$ (dash-dotted and long-dashed lines in Fig. 1b) the benefit increases in a convex manner with increasing habitat area A_i if A_i is rather small, and in a concave manner if A_i is rather large (sigmoid shape). Increasing k_i beyond the value of 2 chosen in Fig. 1b would shift the concave region towards larger values of A_i. The sigmoid shape of the ecological benefit function models an ecological threshold that must be crossed to reach high ecological benefits. The magnitude of habitat area A_i that is needed to cross the threshold is positively related to parameter k_i, so that increasing k_i shifts the threshold towards larger areas A_i.

For $z_i \leq 1$ (solid, dotted and short-dashed lines in Fig. 1b) the benefit B_i increases in a concave manner with increasing habitat area A_i so that the marginal benefit declines with increasing A_i. This case is qualitatively very similar to the case of concave benefit functions in eq. (1a) discussed above.

Initially, each of the two regions has a habitat area of magnitude A_{0i} which may be increased by amounts ΔA_i. The associated costs (depending on the policy instrument this might be purchase of area, conservation payments, etc.) are modelled as

$$C_i = c_{0i}\Delta A_i + e_i\left(\Delta A_i\right)^2, \tag{2}$$

so that cost C_i increases quadratically with increasing habitat area A_i. In economic terms, this means that the marginal cost dC_i/dA_i increases linearly with increasing habitat area A_i, and $2e$ is the slope of that increase. Parameter c_{0i} is the cost of the first unit of increased habitat area. Marginal costs increase because in the decision to conserve some land, the least expensive land parcels are given priority, and with increasing budgets more expensive land parcels are selected. Marginal costs can be shown to increase linearly if the costs of the land parcels are heterogeneous and distributed according to a uniform distribution (Drechsler 2011). For reasons of simplicity, we assume that the financial expenses for conservation, i.e. the budget, equal costs C_i (see Wätzold and Drechsler (2014) and Drechsler (2017) for examples where an efficiency analysis considers budget and costs separately).

The total conserved area in region i then is

$$A_i = A_{0i} + \Delta A_i\,. \tag{3}$$

which determines the benefit B_i according to eq. (1). We assume that the total benefit in both regions is

$$B_{\text{tot}} = B_1 + B_2 , \qquad (4)$$

for an alternative assumption see Wätzold and Drechsler (2005). Based on the above settings and using eq. (1a), Drechsler and Wätzold (2001) analysed the decision problem where a conservation agency must allocate a budget C_{tot} among the two regions to maximise B_{tot}.

The control variable in that static decision problem is the budget share $q \in [0,1]$ that falls into region 1, with $C_1 = qC_{\text{tot}}$ and $C_2 = (1-q)C_{\text{tot}}$ (and $C_1 + C_2 = C_{\text{tot}}$). Depending on the parameters, a cost-effective share q_{opt} exists that maximizes B_{tot} for given C_{tot}.

Dynamics and time-dependence come into play by assuming that the budget becomes available to the conservation agency in two tranches. In a first period the agency can spend a budget of $C^{(1)}$ and in a second period a budget $C^{(2)}$ is available. The corresponding total benefits in the two periods are calculated according to eq. (4) and denoted as $B_{\text{tot}}^{(1)}$ and $B_{\text{tot}}^{(2)}$, and the total intertemporal benefit is assumed to be

$$B = B_{\text{tot}}^{(1)} + rB_{\text{tot}}^{(2)} , \qquad (5)$$

where r is the discount rate.

The task for the conservation agency is to allocate the two budgets $C_{\text{tot}}^{(1)}$ and $C_{\text{tot}}^{(2)}$ among the two regions so that the intertemporal benefit B is maximised. An allocation is represented by $q^{(1)}$ and $q^{(2)}$ where $C_1^{(1)} = q^{(1)}C_{\text{tot}}^{(1)}$ is the budget for region 1 in period 1, $C_2^{(1)} = (1-q^{(1)})C_{\text{tot}}^{(1)}$ is the budget for region 2 in period 1, $C_1^{(2)} = q^{(2)}C_{\text{tot}}^{(2)}$ is the budget for region 1 in period 2, and $C_2^{(2)} = (1-q^{(2)})C_{\text{tot}}^{(2)}$ is the budget for region 2 in period 2.

We consider two settings in this dynamic allocation problem:

(I) 'optimal': the conservation agency knows $C_{\text{tot}}^{(1)}$ and $C_{\text{tot}}^{(2)}$ in the beginning of the first period and chooses $q^{(1)}$ and $q^{(2)}$ to maximise the intertemporal benefit B.

(II) 'myopic': in the beginning of the first period the conservation agency only knows $C_{\text{tot}}^{(1)}$ and chooses $q^{(1)}$ to maximise $B_{\text{tot}}^{(1)}$. Only in the beginning of the second period it learns the budget $C_{\text{tot}}^{(2)}$ for the second period and based on this information chooses $q^{(2)}$ to maximise B.

In the myopic setting, the conservation agency allocates the budget into the two regions based on the size of the currently available budget, as it has no information about the availability of future budgets. This leads to path dependence in a sense that "history matters" (Liebowitz and Margolis 1995): the decision in period 1 on where to allocate the conservation budget $C^{(1)}$ generates conservation conditions that influence the decision in period 2 on where to allocate the conservation budget $C^{(2)}$. As the decisions of the first period cannot be easily reversed for ecological reasons (reversal would create habitat turnover which negatively affects species: Johst et al. 2011) and for economic reasons (it is not straightforward to purchase and sell conservation areas, Lennox et al. 2017), the conservation investment from the first period is "locked-in".

Due to path dependence and the lock-in effect the intertemporal benefit in the myopic setting (B_{myopic}) may be smaller than that in the optimal setting (B_{opt}). An efficiency loss occurs which is measured by

$$L = \frac{B_{\text{opt}} - B_{\text{myopic}}}{B_{\text{opt}}} . \qquad (6)$$

2.2 Model analysis

To analyse the effect of the model parameters on the existence and relevance of path dependencies we randomly sample the model parameter values from uniform distributions (Table 1). We build 10^6 random parameter combinations and for each of them calculate the efficiency loss L. We identify the set $\mathcal{P}$ of all parameter combinations that lead to efficiency losses $L \geq 0.1$ for the scenario of eq. (1a) and $L \geq 0.05$ for the scenario of eq. (1b). We are interested in the statistical properties of the parameter combinations in $\mathcal{P}$. For this we first calculate the means of the model parameters in $\mathcal{P}$ to compare them with the means from the uniform distributions of Table 1. A large difference in these means for some focal model parameter indicates that efficiency losses $L \geq 0.1$ ($L \geq 0.05$) are generated by parameter values that are not any more uniformly distributed but biased towards one of the two bounds of the uniform range. This in turn indicates that this model parameter has a strong influence on the existence of path dependence, and the sign of the difference between the two means indicates whether an increase in the parameter increases or decreases the likelihood of path dependence.

In a second step we aim at detecting interactions between model parameters and calculate pairwise correlations (based on Pearson's correlation coefficient) between the parameters, based on the set $\mathcal{P}$. To identify interactions of three or more parameters we introduce a new approach which is based on the observation that if, e.g., two normalised quantities x and y (with a mean of zero and a standard deviation of one) are strongly positively (negatively) correlated their sum $x + y$ (difference $x - y$) has a comparatively large variation. In Appendix S1 we develop a new procedure that allows analysing combinations of multiple quantities with regard to positive and negative correlations and ranks them through some 'weighted' sum f introduced in Appendix S1. If two model parameters a and b, e.g., have a correlated effect on the likelihood of path dependence, the procedure will generate the result '$\{a + b\}$ best characterises the relationship between parameters a and b', where the plus sign represents the positive correlation (a minus sign would represent a negative correlation). With three model parameters, a, b and c, a typical result might be '$\{a + b - c\}$ best characterises the relationship between the three parameters quantities a, b and c', where $\{a + b - c\}$ stands for 'a is positively correlated with b and negatively correlated with c'. In the analysis we consider interactions of up to four model parameters and identify the three strongest correlations (with highest Pearson's correlation coefficient and/or the highest value of f).

3. Results

3.1 Concave and/or convex benefit functions

We identified 17,680 parameter combinations which lead to efficiency losses L equal or above 0.1. Table 2 shows the means of the parameters in this set $\mathcal{P}$. Some of the means differ from those in Table 1: the means of z_1 and z_2 are increased, those of A_{10} and A_{20} are reduced, and the mean of $C^{(1)}$ is reduced while that of $C^{(2)}$ is increased. The increased means of the exponent z_1 and z_2 mean that efficiency losses are more likely to occur with strongly convex benefit functions (large z). The reason is the strongly increasing marginal benefits associated with strongly convex benefit functions. This implies that (i) the benefit increases fast with increasing budget, it increases faster than the costs which increase only quadratically, and therefore larger budgets should always be allocated into the region with the highest z_i, and that (ii) substantial differences occur between the benefits of the two regions (for given habitat area) even if their z values differ only slightly (Fig. 1a). These two aspects imply that extreme allocations of the budget (all into one region) are most critical if in hindsight it turns out that another allocation with a larger share in the other region would have been better.

Small initial habitat areas A_{01} and A_{02} mean that even if z_1 and z_2 differ, the initial benefits $B_i(A_{0i})$ and the initial marginal benefits $dB_i(A_{i0})/dA_i$ do not yet differ strongly, so the signal for allocating the budget into the region with the higher z_i is weak compared to other signals like costs, so a small budget may be misguided into the region with the lower z_i.

To understand the result regarding the budgets $C^{(1)}$ and $C^{(2)}$, consider that in the myopic setting the conservation agency decides on the first-period allocation only on the basis of $C^{(1)}$. If $C^{(1)}$ is small compared to the total budget $C^{(1)} + C^{(2)}$ then due to the differing cost and benefit functions there is a risk that the cost-effective allocation based on $C^{(1)}$ differs from that based on $C^{(1)} + C^{(2)}$.

Next consider the pairwise correlations between the parameters in $\mathcal{P}$. Both with regard to Pearson's correlation coefficients and our own procedure for detecting correlations (Appendix A), the three strongest correlations are

(i) $z_1 + A_{02}$

(ii) $A_{01} – A_{02}$

(iii) $z_1 – A_{01}$.

Note that these correlations also include their symmetric counterparts, obtained by swapping the region indices 1 and 2, such as, e.g., $z_2 + A_{01}$ for correlation (i), $A_{02} – A_{01}$ for correlation (ii), and $z_2 – A_{02}$ for correlation (iii). Correlation (i) indicates that efficiency losses are likely if the exponent z_1 and the initial habitat area A_{02} are positively correlated. A positive correlation means that a comparatively large value of z_1 is related to a large value of A_{02} and a small value of z_1 is related to a small value of A_{02}. To consider the first case of both parameters being large, according to the benefit function eq. (1), a large A_{02} implies a comparatively large initial marginal benefit in region 2, even if $z_2 < z_1$. A large value of z_1, however, implies that z_1 is likely to be larger than z_2. Consequently, in the myopic setting the large initial marginal benefit in region 2 guides the first-period budget $C^{(1)}$ into region 2 which, however, is likely to have the lower z, and is more effective for larger budgets.

For the case of both z_1 and A_{02} being small the argument is analogous: a small A_{02} implies that the initial marginal benefit in region 2 is likely to be lower than that in region 1, misguiding the first-period budget $C^{(1)}$ into the region which has an exponent z_1 likely to be smaller than z_2.

Since the two cases of both parameters being large and both being small lead to the same conclusion, we consider only one of these two cases in the interpretation of the other correlations below. Analogously, if the two parameters are negatively correlated so that a large value of one parameter coincides with a small value of the other (correlations (ii) and (iii)), we consider only one of the two possible cases. In addition, we consider that if a parameter is high for one region (e.g., large z_1) it is likely (probability above 50%) to be higher than that for the other region (z_2), unless there is some significant correlation between the two parameters (z_1 and z_2).

The (likely) efficiency loss caused by the positive correlation between z_1 and A_{02} (correlation (i)), of course, occurs only if the two initial habitat areas differ (because otherwise both regions would have the same initial marginal benefit), which is indicated by correlation (ii) telling that efficiency losses occur especially if A_{01} and A_{02} are negatively correlated, i.e. when one of them is large and the other one is small.

The negative correlation (iii) between z_1 and A_{01} can be explained in the same way as correlation (i). For instance, a large value of A_{01} implies a high initial marginal benefit in region 1 and in the myopic setting the budget $C^{(1)}$ is likely to be allocated into region 1. This region, however has a small z_1 which calls for allocation of the budget into region 2 (with the probably higher exponent $z_2 > z_1$) in the optimal setting.

The three strongest triple correlations are (again not listing their symmetric counterparts):

(iv) $z_1 - A_{01} + A_{02}$

(v) $z_1 - z_2 - A_{01}$

(vi) $z_1 - z_2 + A_{02}$.

They represent combinations or ‘amplifications’ of the three pairwise correlations above and can be explained in the same way. Correlation (iv), for instance, amplifies correlation (ii) above, so that efficiency losses occur especially if the initial habitat areas are negatively correlated, and if in addition the exponent z_1 in region 1 is negatively correlated with A_{01} (correlation (iii)).

The three strongest quadruple correlations are:

(vii) $z_1 - z_2 - A_{01} + A_{02}$

(viii) $z_1 - c_{02} - A_{01} + A_{02}$

(ix) $z_1 - e_1 - A_{01} + A_{02}$.

Correlation (vii) is again a combination or amplification of the previous correlations. Correlations (viii) and (ix), in contrast, add some new information. Regarding correlation (viii), in the myopic setting the component $z_1 - A_{01} + A_{02}$ is likely to misguide the budget $C^{(1)}$ into region 2 with the higher initial habitat area and marginal benefit. This is amplified by a small initial marginal cost c_{02} (c_{02} is positively correlated with A_{02} in correlation (viii)). In an analogous manner we can explain correlation (ix): in the myopic setting a large slope of the marginal cost e_1 misguides the budget $C^{(1)}$ away from the more costly region 1 although it is likely to have the higher exponent z_1 and would receive the entire budget $C^{(1)} + C^{(2)}$ in the optimal setting.

3.2 Saturating benefit functions

As Table 2 shows, some of the means in set $\mathcal{P}$ differ from those in Table 1. The main differences are that the means of the initial habitat areas, A_{01} and A_{02}, and the budgets, $C^{(1)}$ and $C^{(2)}$, are smaller, with the mean of the first-period budget $C^{(1)}$ being much smaller than that of the second-period budget $C^{(2)}$. Although the means of the exponents z_1 and z_2 are only slightly higher than the means in Table 1, they represent sigmoid benefit functions in which the ecological benefit first increases on a convex manner and later in a concave manner (Fig. 1b). Together with this observation, the relatively small means of A_{01}, A_{02}, $C^{(1)}$ and $C(2)$ indicate that the problem of efficiency losses due to path dependence and lock-in effects occurs especially when the amounts of conserved areas are such that the convex part of the ecological benefit function governs the ecological benefit. By this, similar arguments apply as with concave and/or convex benefit functions.

This is confirmed by the observation that the three strongest pairwise correlations obtained with saturating benefit functions between the parameters in $\mathcal{P}$ are identical to the correlations (i) – (iii) obtained with concave and/or convex benefit functions; and the strongest triple and quadruple correlations are very similar to correlations (iv) – (ix) above.

4. Case study

To illustrate the practical relevance of path dependence and lock-in, we consider the conservation of the endangered Large Blue butterfly, *Maculinea teleius*, in a landscape near the city of Landau in Germany (Drechsler et al. 2007). If the meadows in the landscape (Fig. 2) are managed in a profit-maximising manner, they are mown every year at the end of May and a second time in mid-July. The second cut thus falls into the eclosion period of the butterfly, reducing the species' reproductive success. As a conservation measure, we consider an alternative mowing regime: mowing every second year once at the end of August. This mowing regime maximises butterfly survival in the study region for a given budget, without harming breeding birds (Drechsler et al., 2010). As shown by the authors, the survival of the butterfly is sensitive to the spatial allocation of meadows on which this alternative, butterfly-friendly mowing regime is applied. In particular, butterfly survival increases with increasing spatial aggregation of the butterfly-friendly meadows.

We assume that the butterfly-friendly mowing regime is incentivised through payments from offsets, which are available in Germany (OECD 2016). The offsets compensate for long-term negative impacts on the environment. Therefore, contracts where farmers commit themselves to manage their land in a certain biodiversity-enhancing manner in return to payments, have to be long-term (typically 30 years), too (Treffkorn et al. 2007, OECD 2016). We extent the analysis of Drechsler et al. (2007) with the butterfly-friendly mowing regime of Drechsler et al. (2010) to a dynamic management problem by assuming two periods, each consisting of 15 years, where in the first period a budget is available that allows total payments of €10,000 per annum and in the second period of €20,000 per annum. The budget increase between the two periods mimics the setting of the general model analysis that in the second period more land can be conserved than in the first. Assuming profit-maximising behaviour, landowners with costs below the payment will accept the payment and mow in the butterfly-friendly manner while landowners with higher costs manage their land in the profit-maximising manner.

We further assume that in the west of the study region (left to the vertical dotted line in Fig. 2, termed the western subregion), marginal conservation costs are lower than in the eastern subregion (right to the vertical dotted line in Fig. 2). This is motivated by the assumption of farm houses being located in the more rural eastern subregion, implying that the reduced mowing frequency of the butterfly-friendly mowing regime reduces transport costs from the *distant* meadows in the western subregion to the farm houses (relative to the transport costs associated with the profit-maximising mowing regime which involves more frequent mowing). We add these spatially differentiated transport costs to the conservation costs of Drechsler et al. (2007) by multiplying those costs in the eastern subregion by a factor $b = 2$.

Second, we assume that transport costs are lower if the managed meadows are close to each other. This is relevant especially in the eastern subregion where the meadows are closer to the farm houses, because here a dispersion of the meadows adds relatively more to the transport costs than in the western subregion in which all meadows are associated with rather high transport costs. To model this circumstance in a simple and intuitive manner, we assume that the costs (per hectare) around the point marked by the open circle in Fig. 2 are reduced by

$$\Delta c = -h \exp(-\alpha r) \qquad (7)$$

with h = €400 and $\alpha = (1.25\ \mathrm{km})^{-1}$. At the marked point the costs reduction therefore is Δc = €400 and which declines with increasing distance so that one km from the point it equals about Δc = €180.

The second assumption, together with the fact that the payment scheme induces conservation of the least costly meadows, implies that in the eastern subregion butterfly-friendly meadows will be spatially aggregated, while in the western subregion they will not. Metapopulation theory (Hanski 1999) states that (at least in the absence of correlated environmental stochasticity) the viability of a metapopulation increases with increasing number of habitat patches in a convex manner (e.g., Frank and Wissel 2002), and the strength of this convexity is positively related to the spatial connectivity of the habitat patches (Frank and Wissel 2002). So the viability of the butterfly population in the study region will increase in a convex manner with increasing number of butterfly-friendly meadows, and the convexity is stronger if butterfly-friendly meadows are added in the eastern subregion than in the western subregion.

Together with our first assumption that marginal conservation costs are higher in the eastern subregion than in the western subregion, we are confronted with a typical situation identified in the general model analysis that favours path dependence and lock-in: the ecological benefit functions are convex, and the more convex benefit function is associated with higher marginal conservation costs.

Lock-in arises in the present management problem because the contracts between conservation agency and farmer have a duration of 30 years implying that a meadow conserved in year 1 of the analysis will stay conserved for the next 30 years. The problem of path dependence occurs because in the first 15-year period a rather small conservation budget is available which may favour a different allocation of butterfly-friendly meadows than the larger budget available in the second 15-year period. This change in the cost-effective allocation would call for a reallocation of butterfly-friendly meadows, which however is impossible due to the lock-in.

From the results of the general model analysis we expect that under the myopic setting the conservation agency will, given its small budget in the first period and its aim for cost-effectiveness, allocate the butterfly-friendly meadows in the less costly western subregion – which is achieved by offering conservation contracts for *all* meadows in the study region. In contrast, under the optimal setting where the budget increase to the second period is known it is cost-effective to offer the contracts only for meadows in the *eastern* subregion, because at larger budgets it is more cost-effective to allocate, despite the higher costs, conservation efforts into the region with the more convex benefit function – which in the present case is the eastern subregion.

Figure 3 confirms these expectations. In the first period (lines without symbols) the quasiextinction risk of the butterfly is smaller if conservation contracts are offered for all meadows in the study region (dotted line) than if they are offered only for meadows in the eastern subregion (solid line). So in the myopic setting the conservation agency would offer the contracts for all meadows. In the second period (lines with symbols), in contrast, the quasiextinction risk is lower if the contracts had been offered right from year 1 only for *eastern* meadows (solid line) than if they were offered for *all* meadows over the entire 30 years (dotted line) or if they had been offered for all meadows in the first period and were offered only for the eastern meadows in the second period (dashed line). Altogether, if only the first period is considered it is more cost-effective to offer the contracts for all meadows while if the longer future is considered it is more cost-effective to offer them only for meadows in the eastern subregion.

As the case study only served to illustrate the potential relevance of our general analysis for real-world conservation, a systematic analysis of the driving factors of the results is beyond the scope of this paper. However, we analysed two alternative scenarios without (i) reduced differences in the strengths of convexity (by largely eliminating the spatial clustering of butterfly-friendly meadows in the eastern subregion and setting $\alpha = (0.125 \text{ km})^{-1}$) and (ii) reduced differences in the marginal conservation costs between the two subregions (by reducing b to 1.5), and observed no path dependence: offering the contracts for *all* meadows always minimised the quasiextinction risk. This indicates that the path dependence observed in the case study indeed results from the described positive correlation between marginal conservation costs and strength of convexity in the ecological benefit function.

5. Summary of results and discussion

Efficiency losses due to path dependence and lock-in effects are likely if there are signals that misguide the first-period budget into a region that is suboptimal in terms of cost-effectiveness if both time periods were considered right from the beginning. These wrong signals are mainly sent from the marginal costs and benefits. Large initial costs and/or small initial marginal ecological benefits in one region are likely to guide the first-period budget into the other region. This other region, however, may have a less strongly increasing ecological benefit function if both time periods and both budgets were considered.

In our model, this occurs especially if

(i) the ecological benefits functions are strongly convex, so that the benefit increases at an increasing rate,

(ii) level and slope of marginal costs are small in the region with the less convex benefit function, so that the first-period budget is misguided into the region which in the long run has the lower ecological benefit,

(iii) the initial habitat area, and thus the initial marginal benefit is small in the region with the more convex benefit function, so that the first-period budget is misguided into the other region which in the long run has the lower ecological benefit.

The conservation relevance of the findings is demonstrated by a case study where offset payments are applied to butterfly conservation near the city of Landau, Germany.

Naturally, the problem of path dependence occurs if the budget for the first period is substantially smaller than the total budget available for both periods. If it was almost as large as the total budget the allocation signal for the first-period allocation would likely to be the same as that for the allocation of the total budget. On the other hand, it is plausible (not analysed systematically in this paper) that an extremely small first-period budget would not lead to large efficiency losses, because even if it was allocated into the wrong region, the associated 'waste of money' would be small.

The insights from our model can be generalised to make them fruitful to a broader conservation context. The model results indicate a principle structure where in a situation with several conservation projects and uncertainty over future budgets, path dependence and lock-in effects with efficiency losses are likely to occur: This is the case if marginal net benefits (benefit minus costs) of some projects in the first period are high but in later period(s) low and for other projects the opposite applies. Myopic concerns of cost-effectiveness (under uncertainty) then suggest allocating resources in the first type of projects whereas with hindsight and over a long time the opposite allocation might have been the more cost-effective option. Our case study suggests that such a structure might not be uncommon in conservation decisions, calling for more research on path dependence and lock-in effects in biodiversity conservation, the efficiency losses that arise and policy responses to avoid them.

Although these conclusions are derived from an analysis with two periods, we believe that in their general sense they are valid also in conservation management problems with more than two periods. Nevertheless, extending the analysis two more than two periods would be an interesting matter of future research.

A straightforward policy recommendation from our analysis is that uncertainty over future budgets should be minimized to the extent possible to avoid efficiency losses due to path dependence and lock-in effects. This conclusion – based on a conceptual model – is in line with calls from practitioners in several European countries who consider uncertainty over future budgets a main impediment for cost-effective conservation activities (Wätzold et al. 2010). This indicates a high relevance of the issue of budget uncertainty and that better conservation outcomes can be achieved if information about future conservation budgets is available at an early stage.

In our opinion, there is substantial potential for further research to understand under what ecological and economic conditions path dependence and lock-in effects in biodiversity conservation occur and how conservation policy responses should look like. In our case, budget uncertainty leads to path dependence and lock-in effects. However, other factors may also favour or hinder their occurrence. A possible factor is the flexibility of policy instruments to respond to changing ecological and societal circumstances. For example, some people argue that conservation banking may be a flexible policy instrument able to respond to change (Johst et al. 2011, Wende et al. 2018) whereas other policy instruments such as conservation easements are criticised for lacking flexibility (Rissman et al. 2013). In how far inflexibility of policy instruments contributes to path dependence and lock-in effects is a matter of further research and we hope this paper can stimulate this and related debates. These debates seem important from a conservation point of view, as our analysis suggests that if path dependence and lock-in effects are not considered, efficiency losses may occur resulting in a waste of scarce conservation resources (cp. Ferraro and Pattanyak 2006, Cong and Brady 2012).

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Tables

Table 1: Ranges for the model parameters.

Parameter	Meaning	Minimum	Maximum	Mean
z_i	Exponent benefit function (eq. 1a)	0	5	2.5
k_i	Threshold in sigmoid benefit (eq. 1b)	0	10	5
c_{0i}	Offset marginal cost function (eq. 2)	0	1	0.5
e_i	Slope marginal cost function (eq. 2)	0	5	2.5
A_{0i}	Initial conserved area region *i* (eq. 3)	0	10	5
$C_{\mathrm{tot}}^{(1)}$	Budget period 1	0	10	5
$C_{\mathrm{tot}}^{(2)}$	Budget period 2	0	10	5
r	Discount rate for benefit (eq. 5)	0	0.1	0.05

Table 2: Means of the parameter values in the set $\mathcal{P}$ of parameter combinations that lead to efficiency loss $L \geq 0.1$ (concave and/or convex benefit functions, scenario a) and $L \geq 0.05$ (saturating benefit functions, scenario b), respectively. In parentheses the comparison with the means from the uniform distributions of Table 1.

Parameter	Mean (concave/convex)	Mean (saturating)
Benefit exponent z_1	3.38 (> 2.5)	2.77 (> 2.5)
Benefit exponent z_2	3.39 (> 2.5)	3.04 (> 2.5)
Threshold k_1	-	5.80 (≈ 5)
Threshold k_2	-	5.92 (≈ 5)
Initial marginal cost c_{01}	0.51 (≈ 0.5)	0.52 (≈ 0.5)
Initial marginal cost c_{02}	0.51 (≈ 0.5)	0.53 (≈ 0.5)
Slope marginal cost e_1	2.43 (≈ 2.5)	2.95 (> 2.5)
Slope marginal cost e_2	2.42 (≈ 2.5)	2.74 (≈ 2.5)
Initial habitat area A_{01}	3.72 (< 5)	1.84 (< 5)
Initial habitat area A_{02}	3.68 (< 5)	1.47 (< 5)
Budget period 1 $C^{(1)}$	3.25 (< 5)	0.96 (< 5)
Budget period 2 $C^{(2)}$	6.56 (> 5)	1.97 (< 5)
Discount rate r	0.05 (= 0.05)	0.05 (= 0.05)

Figures

Figure 1: Concave and convex benefit functions (panel a) for different values of z_i (solid line: $z_i = 0.2$, dotted line: $z_i = 0.5$, short-dashed line: $z_i = 1$, dash-dotted line: $z_i = 2$, long-dashed line: $z_i = 5$). Saturating benefit functions (panel b) for $k_i = 2$ and different values of z_i (values as in panel a).

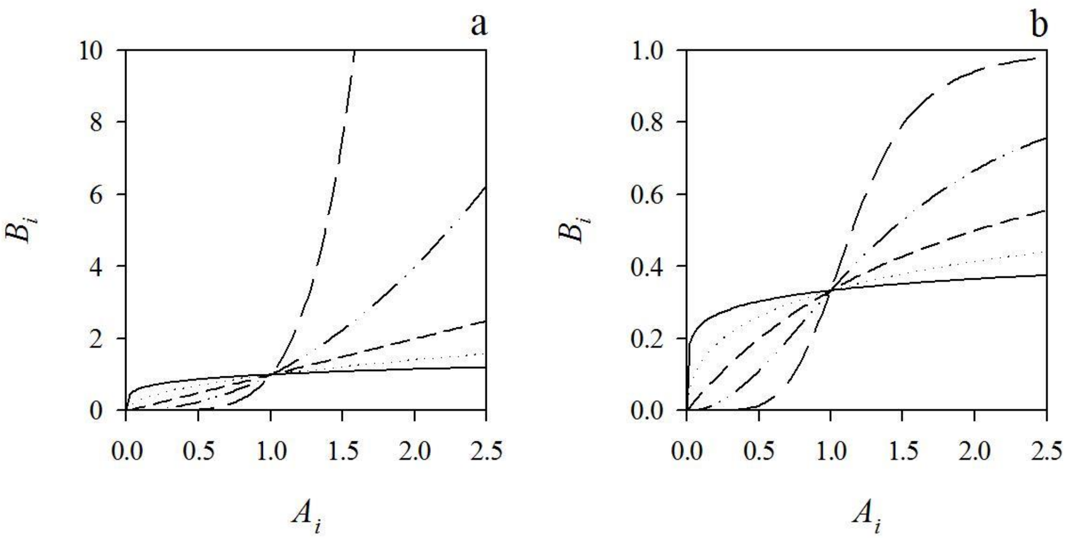


Figure 2: Model landscape (black: settlements, dark grey: forest, light grey: open land, white: meadow). Source: Drechsler et al. (2007). The dotted line separates the eastern subregion defined in section 4 from the western subregion, and the open circle marks the location at which the cost reduction introduced by eq. (7) is maximal.

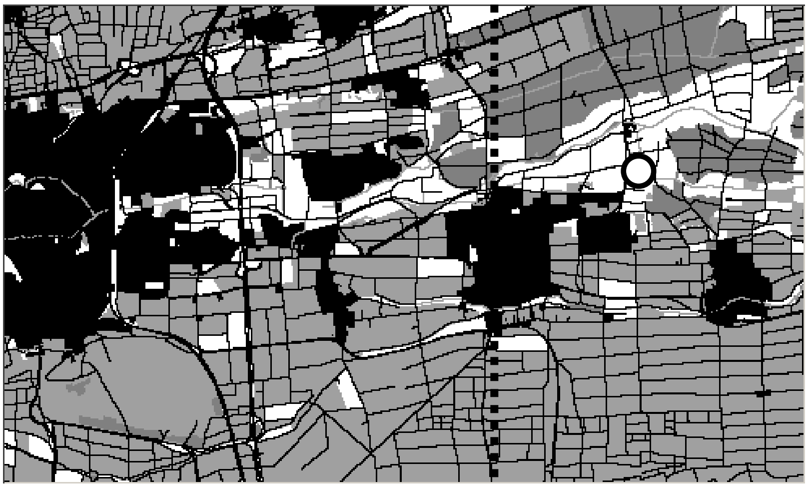
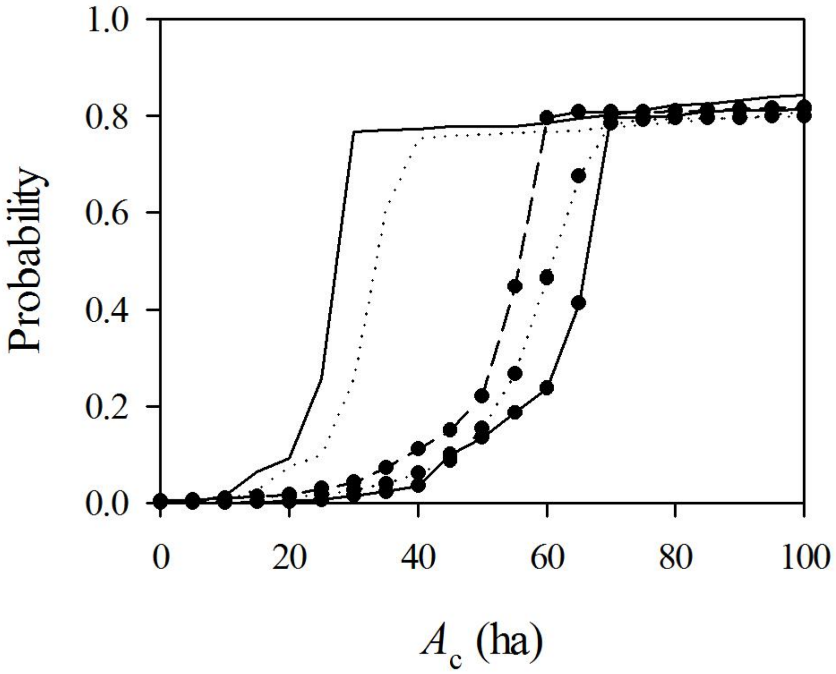


Figure 3: Quasiextintions risk: probability of the area occupied by the butterfly falling below the threshold A_c within a 15-year time period as a function of Area. Lines without symbols: first period (years 1 – 15); lines with symbols: second period (years 16 – 30). Solid lines: optimal setting; dotted lines: myopic setting with payment offered to all farmers in both periods; dashed line: myopic setting with payment offered to all farmers in the first period and only to the farmers in the eastern part of the region in the second period.



Appendix S1: Development of a procedure to detect interactions among multiple quantities

The development of the procedure starts with the observation that the variation in the sum of two normalised quantities *a* and *b* (with zero means and standard deviations of one) monotonically increases with increasing Pearson's correlation coefficient between the two quantities. To understand the reason, assume *a* and *b* to be strongly positively correlated (Pearson's correlation coefficient close to 1). This means that large *a* are associated with large *b* and small *a* are associated with small *b*. Consequently, the sum $a + b$ will have a rather high standard deviation (close to 2 given *a* and *b* are normalised as described). In contrast, if *a* and *b* were uncorrelated (with zero Pearson's correlation coefficient) a large value of *a* could well occur with a medium or small value of *b* and the standard deviation of $a + b$ would be lower. In the case of negatively correlated *a* and *b* (Pearson's correlation coefficient of –1) a large value of *a* would be associated with a small value of *b* and a small value of *a* with a large value of *b*, implying that the standard deviation of $a + b$ would be minimal (close to 0 given the normalization described above). Figure A1 shows the relationship between the standard deviation of the sum $a + b$ and Peason's correlation coefficient between *a* and *b*.

In an analogous manner one can show that the standard deviation of the difference $a – b$ increases with decreasing Pearson's correlation coefficient between *a* and *b* and, in particular, has a minimum value of 0 if *a* and *b* are perfectly positively correlated and a maximum value of 2 if *a* and *b* are perfectly negatively correlated.

To consider interactions between three or more quantities, $a_1 \ldots a_N$, we first normalise the a_i, so each of them has zero mean and a standard deviation of one, and build all possible functions

$$f(a_1,...,a_N; w_1,...,w_N) = w_1 a_1 + w_2 a_2 + ... + w_N a_N \quad \text{(A1)}$$

where each w_i can take values of –1, 0 or +1. By this, each quantity a_i is combined with the other quantities a_j ($j \neq i$) either in an additive manner ($w_i = 1$), a subtractive manner ($w_i = –1$) or not at all ($w_i = 0$), and by systematically varying all w_i within their ranges all combinations of positive and negative correlations between the quantities $a_1 \ldots a_N$ are considered. We restrict our analysis to a maximum of four interacting model parameters, i.e., $\Sigma_i|w_i| \leq 4$. We rank the combinations $\{w_i\}$ with regard to the magnitude of function f and identify the combinations with the highest values of f.

Figure A1: Standard deviation of the sum $a + b$ of two quantities a and b (each with zero mean and standard deviations of one) versus Pearson's correlation coefficient between a and b. The statistics are calculated on the basis of 1000 samples of a and b.