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29 September 2022

# The ”climate adaptation problem” in biodiversity conservation: the role of reversible conservation investments in optimal reserve design under climate change

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*Parts of this work are available in an earlier version of this work. That version can be found under https://mpra.ub.uni-muenchen.de/114503/*

## ABSTRACT

Existing reserve networks become less suitable as species' ranges shift under climate change. Climate change hence changes the comparative advantage of some sites over others with respect to ”producing” habitat. In order to maintain cost-effectiveness, reserve networks therefore have to be adapted. However, policy instruments may restrict the adaptation potential of reserves. For example, land purchase by a conservation agency typically constitutes an irreversible investment, as previously purchased sites are not sold. In order to adapt conservation to climate change, one may hence consider land purchase as a partially reversible investment, in which sites may be sold in order to liquidate funds for new purchases. However, negative ecological consequences (habitat turnover) are an important disadvantage of selling. Here, we use a climate-ecological-economic model to assess the trade-off between irreversible conservation investments (with limited adaptation potentials to climate change) and partially reversible conservation investments (which may incur higher habitat turnover). We apply the model to a conceptual case study of conserving different habitat types to assess the trade-off for different funding levels. Our results show that the advantage of selling in terms of habitat protection is large when no additional funds are available and decreases as the amount of additional capital increases. Moreover, we find that due to climate change, habitat turnover occurs even in a static reserve network, but the loss in habitat permanence when allowing for sale is smallest for the most threatened habitat type. We hence identify a new trade-off in the evaluation of land purchase for the climate adaptation problem in biodiversity conservation: while not allowing for sale mainly benefits the habitat permanence of the expanding habitat type, allowing for sale mainly benefits the outcome for the contracting habitat type.

*Keywords:* Biodiversity; climate adaptation; climate-ecological-economic model; spatial flexibility; habitat permanence; habitat turnover; irreversible investment; investment with costly reversibility; RD-problem; selling reserve sites

## 1 INTRODUCTION

The location of nature reserves needs to be adapted in order to conserve biodiversity in the future (Heller and Zavaleta, 2009; Vincent et al., 2019) because climate change causes range shifts in species and potential habitat sites (Ponce-Reyes et al., 2017; Campos-Cerqueira et al., 2021;

Dasgupta, 2021). From an economic perspective, climate change may thus induce changes to the comparative advantage of some sites over others: if climate change leads to a relative increase (decrease) in the ecological potential of new (former) sites, the optimal reserve network may change. Here, we consider the optimal reserve network to be the cost-effective network, and define cost-effectiveness as maximising conservation benefits for given costs (Wätzold, 2014). To maintain cost-effectiveness and prevent the loss of certain habitat types under climate change, the reserve network may therefore have to be adapted (Gerling and Wätzold, 2021; Ranius et al., 2022). There are a range of studies investigating how to expand nature reserves to maintain target habitats under climate change considering the specific conditions of case studies (Pyke and Fischer, 2005; Fung et al., 2017; Graham et al., 2019; Lawler et al., 2020). However, this research typically does not consider that conservation activities are implemented within the restrictions of policy instruments, and that these restrictions may limit the adaptation.

In order to adapt biodiversity conservation to climate change, understanding the suitability of policy instruments for this adaptation is hence of great importance. Given that cost-effective conservation under climate change requires some ”spatial flexibility” to adapt the location of reserve sites, policy instruments need to be evaluated differently when considering the climate adaptation problem (in comparison to the problem of biodiversity conservation under static climatic conditions) (Gerling and Wätzold, 2021). We believe that economic research plays an important role in assessing policy instruments for the climate adaptation problem for biodiversity conservation - just as economic research has contributed to designing policy instruments for the problem of biodiversity conservation under static climatic conditions (e.g., Armsworth et al. (2012), Wätzold et al. (2016), and Simpson et al. (2021)). However, so far, there is little economic research on the design of policy instruments for cost-effective climate adaptation for biodiversity conservation: Gerling and Wätzold (2021) provide an evaluation framework for policy instruments for biodiversity conservation under climate change. Schöttker and Wätzold (2022) assess the cost-effectiveness of different governance modes for biodiversity conservation under climate change. Finally, Huber et al. (2017) simulate the outcome of agri-environment schemes under climate change and Gerling et al. (2022a) examine changes in the cost-effective conservation measures of an agri-environment scheme over time due to climate change.

In this paper, we examine land purchase by a conservation agency to create reserves as a common policy instrument for biodiversity conservation (Armsworth et al., 2006; McDonald-Madden et al., 2008; Schöttker et al., 2016; Hardy et al., 2018). Typically, reserves may be expanded but reserve sites are rarely sold (Fuller et al., 2010; Lennox et al., 2017): selling reserve sites is often not permitted as habitat turnover is an important negative ecological consequence (Ando and Hannah, 2011; Lennox et al., 2017; Gerling and Wätzold, 2021) and due to transaction costs such as taxes and the identification of suitable sites for selling (Schöttker and Wätzold, 2018). In the reserve design problem (RD-problem), regulations prohibiting the sale of existing reserve sites thus render the RD-problem a problem of irreversible investments (Ando and Hannah, 2011; Traeger, 2014; Lennox et al., 2017). In order to increase flexibility for climate adaptation, one may therefore consider increasing the degree of reversibility: generally, investments may range from irreversible investments (Arrow, 1968; Pindyck, 1988) to fully reversible investments (which imply full recoverability of initial investment costs (Davis and Cairns, 2017)). In between these extremes, investments may be partially reversible, i.e. reversible at a cost (Baldwin, 1982; Abel and Eberly, 1996; Hartman and Hendrickson, 2002). Considering the RD-problem, allowing for sales of existing sites can be seen as a case of finding the optimal investment decision in the case of costly reversibility, as transaction costs do not allow for full recoverability of initial investment costs (Verbruggen, 2013; Drechsler and Wätzold, 2020). Considering conservation investments for climate adaptation, the decision maker hence faces a trade-off between an irreversible investment problem (with limited flexibility for adaptation) and an investment with costly reversibility (with both positive and negative ecological consequences arising from the increased flexibility).

Recent research provides some evidence that the advantages of selling may outweigh the costs under changing climatic conditions, albeit cautioning against general recommendations of allowing for selling (Alagador et al., 2014, 2016). In this paper, we examine two alternative versions of land purchase for the climate adaptation problem in biodiversity conservation: ’sale’ vs. ’no sale’. We explicitly assess the gains in cost-effectiveness (focusing on habitat area) achieved by the ’sale’ policy as well as the resulting losses in habitat permanence by comparing it to the ’no sale’ policy. Overall, we aim to gain some conceptual understanding on whether and when allowing for sale may be warranted to contribute to the limited economic research on the design of cost-effective policy instruments for climate adaptation for biodiversity conservation.

In order to address this question, we apply a climate-ecological-economic (CEE) modelling approach to assess the trade-off between the ’sale’ and the ’no sale’ policies. We apply the model to a conceptual landscape of potential reserve sites. Potential reserve sites differ in their suitability for different habitat types both spatially (some habitat types are more likely to occur on high elevations, others on lower elevations) and temporally (climate change influences the suitability of a site for the different habitat types over time). The potential spatial distribution of the different habitat types therefore changes under climate change and includes habitat types that expand and others that contract. We consider three habitat types with different characteristics in order to illustrate this. Additionally, the opportunity costs of conservation are spatially heterogeneous.

In our results, we show how the ecological outcome of the reserve network changes under climate change and compare the outcomes of the ’sale’ and the ’no sale’ policies. We consider different budget constraints to examine whether the size of the budget has an influence on the comparison. Finally, we examine the degree of habitat turnover that results from the increased flexibility and the cost of reducing habitat turnover when selling is permitted. Overall, we hence aim to gain an understanding on the trade-off between allowing for sale (which provides flexibility at a cost in terms of habitat turnover) and not allowing for sale (which maximises habitat permanence but does not account for changes in comparative advantages of sites over time) for adapting biodiversity conservation to the challenges of climate change.

# 2 THE ”CLIMATE ADAPTATION PROBLEM”: CONCEPTUAL CONSIDERATIONS

## 2.1 Multi-objective optimisation in the biodiversity conservation problem

In the economic literature, a typical definition of cost-effectiveness in the context of biodiversity conservation is maximising conservation outcomes for given costs (Wätzold, 2014; Grand et al., 2017) or reaching a certain conservation target (such as habitat area or a set of species to protect) at minimum costs (Ando et al., 1998). In some cases a single, clearly defined conservation objective (such as a single target species to be conserved) may be determined to define the resulting maximisation or minimisation problem.

However, it is likely that the decision maker cares not just about a single conservation objective but several (e.g., several species or habitat types). In this case, the decision maker may hence face trade-offs between the different objectives. This could be depicted as a production possibility frontier (PPF). For example, Nalle et al. (2004) consider both economic and ecological objectives and generate a three-dimensional PPF considering two different conservation objectives (two woodland species) and timber production - however, a PPF focusing on different habitat types could also be imagined. The problem is then to determine which of the Pareto-efficient points on the PPF maximises welfare. If the decision maker's indifference curve, and hence, marginal rate of substitution between the different habitat types was known, the optimal solution could be determined analytically. However, the decision maker's indifference curve is unlikely to be known in reality. For specific case studies, one could use surveys such as choice experiments to gain some understanding of how different conservation objectives are valued (see for example Faccioli et al. (2015)).

At a more generic level, one would need an optimisation procedure that considers the different conservation objectives and which captures preferences that seem likely. For example, one could value each objective equally (see Önal (2004) for a general model description). In order to consider that very small habitat areas have a high risk of disappearing due to stochastic events, one could additionally set threshold values which need to be passed for each objective in the optimisation (Önal, 2004; Johst et al., 2015). One may also consider optimisation procedures that value the different objectives differently. One typical example is the *maximin* approach (Montoya et al., 2020), which focuses on the most threatened species or habitat type.

## 2.2 Additional complexities under climate change

Under climate change, multi-objective optimisation procedures may need to be adapted to account for possible changes on both the supply side (referring to what conservation objective may be reached how) and the demand side (referring to possible changes in indifference curves and hence, changes in which of the efficient points on the PPF is considered 'optimal').

Regarding the supply side, there are two main factors that need to be considered. First, the spatial distribution of habitat types is likely to change, implying that the conservation outcome of a static reserve network changes over time (Lewis and Polasky, 2018). When aiming for constant values for the conservation objective, one would therefore have to adapt the site selection over time. Second, the relative occurrence of habitat sites changes as some habitat types are likely to expand and others are likely to become more threatened. This may be visualised as changes to the PPF (Figure 1): both the extreme points of the PPF of only conserving a single habitat type and the shape of the function between these extremes may change as some habitat types become scarcer and others less so. For example, the maximum of a chosen conservation objective may move closer to the origin as the respective habitat type becomes more threatened (habitat type A in Figure 1 moves from $A_{max1}$ to $A_{max3}$), while for another conservation objective the maximum value moves further outwards as the respective habitat type becomes less threatened under climate change (habitat type B in Figure 1 moves from $B_{max1}$ to $B_{max3}$). The opportunity costs of conserving habitat type A in terms of habitat type B therefore increase as the slope of the PPF (marginal rate of transformation) becomes steeper.

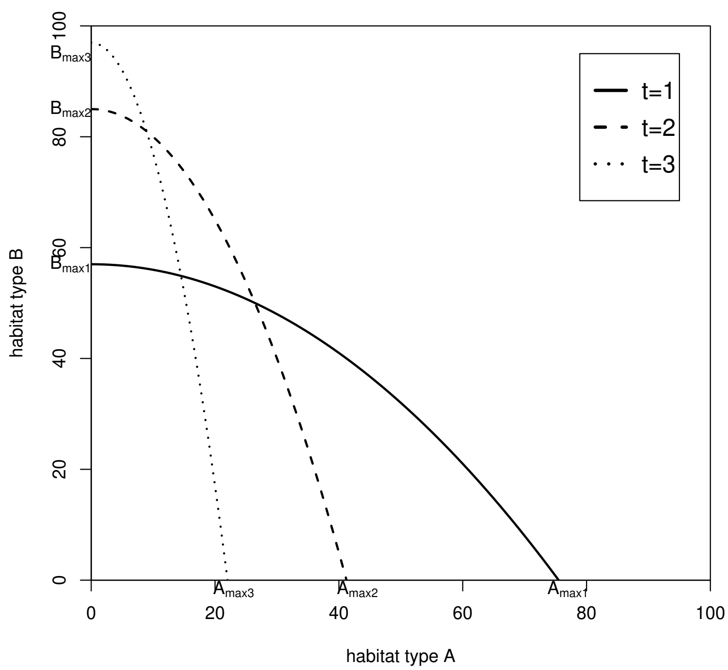


**Figure 1.** Hypothetical changes to production possibility frontiers at time steps $t \in \{1,2,3\}$ for two habitat types A and B.

Typical optimisation procedures based on the standard definitions of cost-effectiveness may not capture these dynamics adequately. When aiming to conserve a pre-defined set of habitat types at minimum costs, one needs to consider that some habitat types may disappear, and the pre-defined objective may no longer be viable. When considering certain minimum threshold values in order to avoid very small habitat areas, these threshold values may not capture the changing scarcity of habitat types adequately. For example, a habitat type may still be conserved, but a formerly sensible threshold value may no longer be achieved as the habitat type becomes more threatened. In the hypothetical example depicted in Figure 1, a threshold value of 25 units may have been considered sensible initially, as this is only a fraction of the maximum area of either habitat type. However, in time step 3, this threshold cannot be reached anymore for habitat type A. Nonetheless, the habitat type can still be conserved if the threshold value was adapted to take into account that it becomes more threatened.

Considering the demand side, it is unclear whether climate change influences how chosen habitat types or species are valued, as there is little research on the topic (see Lundhede et al. (2014) for an exception). When considering the *maximin* approach as a heuristic to represent possible preferences, one needs to consider that the habitat type which identifies as ’most threatened’ may change over time. The *maximin* approach may therefore have to be adapted under climate change in order for the optimisation procedure to consider possible future developments in the rareness of the habitat types.

## 3 THE CEE MODEL

We have developed a CEE model able to address the challenges discussed above. In this section, we describe the CEE model, the decision problem of the conservation agency and the policy scenarios. The basic CEE model has been published previously as Gerling et al. (2022b) - we hence refrain from repeating the details of the mathematical notations of the model in this article but rather provide a brief overview of the model and focus on the adaptations of the model to assess the ’sale’ and ’no sale’ policies.

We consider a two-step optimisation procedure. In the first step, the optimal reserve network for current climatic conditions is generated. In the following dynamic optimisation, this reserve network is adapted over time to account for climatic changes.

### 3.1 Modelling of the landscape, habitat types and climate change

We consider a conceptual landscape consisting of a valley, plains of medium elevation and a mountain. This landscape is divided into 200 cells (compare Fig. 2 and see Gerling et al. (2022b) for details on the construction of the landscape). In this landscape, three different habitat types exist ($H_k$: $H_1$, $H_2$, $H_3$): $H_1$ represents a habitat type predominantly present in low elevations, $H_2$ can mainly be found in the plains, and $H_3$ represents a mountain habitat type located in high elevations. Each grid cell hence has a specific utility value for each of the habitat types, $h_{kit}$, which is particularly high in the respective ideal zone (e.g. in the valley for $H_1$). Moreover, each cell has specific conservation costs as opportunity costs are typically spatially heterogeneous (Lewis and Polasky, 2018).

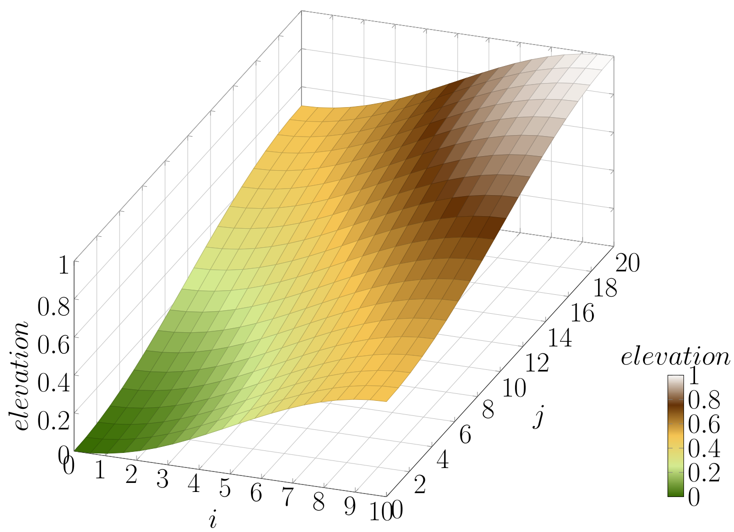


**Figure 2.** Landscape grid and grid cells, coloured by elevation level visualising the topography of the landscape.

When conserving a grid cell, the habitat types appear on this grid cell according to their respective utilities $h_{kit}$ instantly (see Gerling et al. (2022b) for details on the underlying functional relationship). This means that conserving a specific grid cell is likely to lead to 2 or 3 habitat types being conserved, but depending on the utilities $h_{kit}$ conserving a grid cell $i$ may lead to higher outcomes for some habitat types than for others. For example, conserving a grid cell in the plains may lead to all three habitat types being conserved, but the largest portion of the grid cell will be covered by habitat type $H_2$ as the plains provide only sub-optimal conditions for $H_1$ and $H_3$. Any non-conserved grid cell does not provide any habitat $H_k$.

Climate change changes the suitability of the grid cells for the different habitat types. The utility $h_{kit}$ is hence time-dependent. Importantly, climate change impacts each habitat type differently, representing different possible changes in comparative advantages: the cells' utility for habitat type $H_1$ (which is initially high in the valley) improves generally over time and leads to $H_1$ potentially covering an increasingly large portion of the landscape. Hence, it becomes increasingly present in areas with higher elevation. The cells' utility for $H_2$ (which is initially high in the plains) generally decreases, leading to habitat type $H_2$ to shrink in its potential extent. Cells of higher altitude however will face an increase in utility for habitat type $H_2$, meaning that the potential habitat sites tend to move "uphill" towards higher elevations. The cells' utility for $H_3$ (for which the potential habitat sites are initially mainly found on the mountains) also decreases over time. Thus, the potential extend of $H_3$ also shrinks over time and eventually almost disappears as a further upwards movement is impossible. Figure 3 illustrates the suitability of each habitat for all elevation levels for time steps $t = \{1, 5, 9, 13\}$. While the model landscape is purely conceptual, it represents typical habitat shifts observed in reality in which species' ranges shift uphill, which means that mountain top habitats become particularly threatened (see for example Lamprecht et al. (2018)).

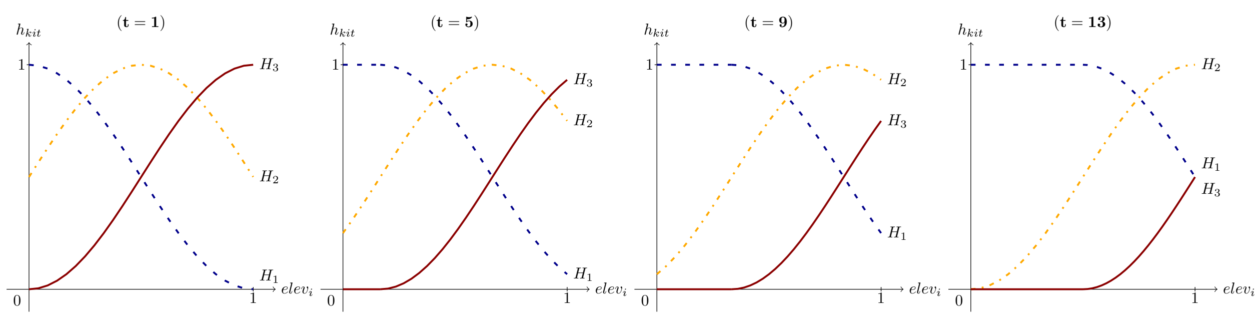


**Figure 3.** Utility level $h_{kit}$ of a cell $i$ at time steps $t \in \{1, 5, 9, 13\}$ for all three habitat types $k \in \{1, 2, 3\}$.

Each time step $t$ represents a five-year period. Overall, we consider $T$=13 time steps: $t = 1$ represents the initial optimisation problem which generates the initial reserve network, while the subsequent time steps represent the time frame in which the reserve network needs to be adapted to climate change ('dynamic optimisation'). This implies that in the dynamic optimisation, we consider a period of 60 years.

## 3.2 Decision problem: optimal allocation of reserve sites

We assume that a conservation agency aims to conserve all three habitat types. We first apply a *maximin* approach in order to ensure that the conservation agency initially owns the optimal reserve network that conserves all habitat types given a budget constraint of $500\mu$ (where $\mu$ indicates monetary units). This budget is approximately 7% of the value of all potential reserve sites in the landscape. Moreover, we ensure that the reserve network is connected by only allowing sites within the Moore neighbourhood of another site (Gray, 2003) to be added to the reserve network.

Based on this set-up, we then determine the optimal time series of reserve networks in a dynamic optimisation. In this optimisation we consider changes in comparative advantages over time: as some sites become more ”productive” in producing a specific habitat type, others become less productive as the spatial distribution of habitat types shifts and the relative occurrence of habitat types changes. We determine the optimal allocations of reserve sites over time for the ’sale’ and ’no sale’ policy separately and then assess potential gains in cost-effectiveness and increases in habitat turnover between the two policies in the results section.

In the dynamic optimisation, we again apply a *maximin* approach to maximise the minimum value achieved by each habitat type at any time $t$. To do so, we determine the point where the PPF touches the axis for each habitat type at time $t$ to determine the maximum outcome that may be reached for each habitat type in time $t$. We use these values as goals and apply a goal programming approach in which we minimise the distance from the goals. We assume that the decision maker has perfect information on future developments and may hence take future developments into account in current decisions.

In the optimisation, the site selection is constrained by the available budget in time $t$, $B(t)$:

$$B(t) \geq \sum_{i \in N} (1+a) * p_i * b_{it} \quad \forall t \in T \tag{1}$$

The cost of purchasing site $i$ is equal to its price, $p_i$ plus transaction costs $a$. $b_{it}$ is a dummy variable indicating whether site $i$ is purchased in time $t$.

The available budget differs between the 'sale' and the 'no sale' strategy:

$$
\begin{aligned}
B(t) =& k(t) + c(t-1) * (1+r)^5 + \\
& (1+r)^{2.5} * \sum_{i \in N} (1-a) * p_i * s_{it} \quad \forall t \in T
\end{aligned}
\tag{2}
$$

The budget may consist of an 'adaptation budget' $k(t)$ received in time $t$, any budget remainders of the previous period $c(t-1)$ including corresponding interest payments, and - under the 'sale' policy - funds from selling reserve sites. Funds from selling reserve sites consist of the price of site $i$, $p_i$ net of transaction costs $a$. Note that $s_{it}$ is a dummy variable taking the value 1 when site $i$ is sold in time $t$ and 0 otherwise. Under the 'no sale' policy, $s_{it}$ is hence always 0. For simplicity, we assume that all sites are sold in the middle of each 5-year period.

Finally, the 'sale' policy is subject to an additional constraint in order to ensure that reserve sites do not become isolated: we only allow a site to be sold if at least one other reserve site lies within its Moore neighbourhood (cp. Appendix A).

### 3.3 Policy scenarios

We compare the 'sale' and the 'no sale' policies for different budget constraints in order to see whether the size of the budget has an influence on whether the 'sale' or 'no sale' strategy is preferable. Specifically, we consider that the agency may have no, a low or a high adaptation budget $k(t)$ to adapt the reserve network in every time step $t \in \{2,...,T\}$ of the dynamic optimisation. In the 'low funding' case, the size of the regular 'adaptation payments' is $50\mu$ for each five-year period, in the 'high funding' case it is $100\mu$.

We therefore consider 6 policy scenarios (Table 1):

| | $k(t) = 0\mu$ | $k(t) = 50\mu$ | $k(t) = 100\mu$ |
|---|---|---|---|
| **’no sale’** | no sale - no funding | no sale - low funding | no sale - high funding |
| **’sale’** | sale - no funding | sale - low funding | sale - high funding |

**Table 1.** Overview of the 6 policy scenarios.

# 4 RESULTS

## 4.1 ’Sale’ vs. ’no sale’ policy: cost-effectiveness comparison

Figure 4 shows how the different habitat types develop over time for the ’sale’ and ’no sale’ policies. It can be seen that generally, habitat $H_1$ is initially the most threatened but increases over time in all 6 scenarios. Habitat $H_2$, which we expect to move ’uphill’, increases in its extent in most scenarios. However, Figure 4a shows that when the initial reserve network cannot be adapted (i.e., no additional capital is provided and sales are prohibited), $H_2$ loses. Finally, habitat $H_3$ becomes the most threatened habitat type in all scenarios under climate change. However, when the reserve network may be expanded by providing sufficient additional capital and/ or allowing for sales, the loss in $H_3$ is less pronounced.

Comparing the outcomes of the ’sale’ and the ’no sale’ policy directly, one can see that the advantage of the ’sale’ policy decreases as the amount of additional funding increases: when no additional capital is available, allowing for sales is the only option of adapting the reserve network. The ’sale’ strategy then improves the final outcome for the most threatened habitat type $H_3$ by a factor of 5.8 (from 0.8 (Figure 4a) to 4.6 (Figure 4d)). In the low funding case, the ’sale’ strategy only improves the outcome by a factor of around 1.1 (from 6.6 (Figure 4b) to 7.2 (Figure 4e)), while the outcome in the high funding case is comparable for both policies (Figure 4c and f).

Hence, the ’sale’ option is preferable over the ’no sale’ option in the ’no funding’ and ’low funding’ cases, especially for the most threatened habitat type $H_3$. With increasing amounts of additional funding the advantage of the ’sale’ option decreases.

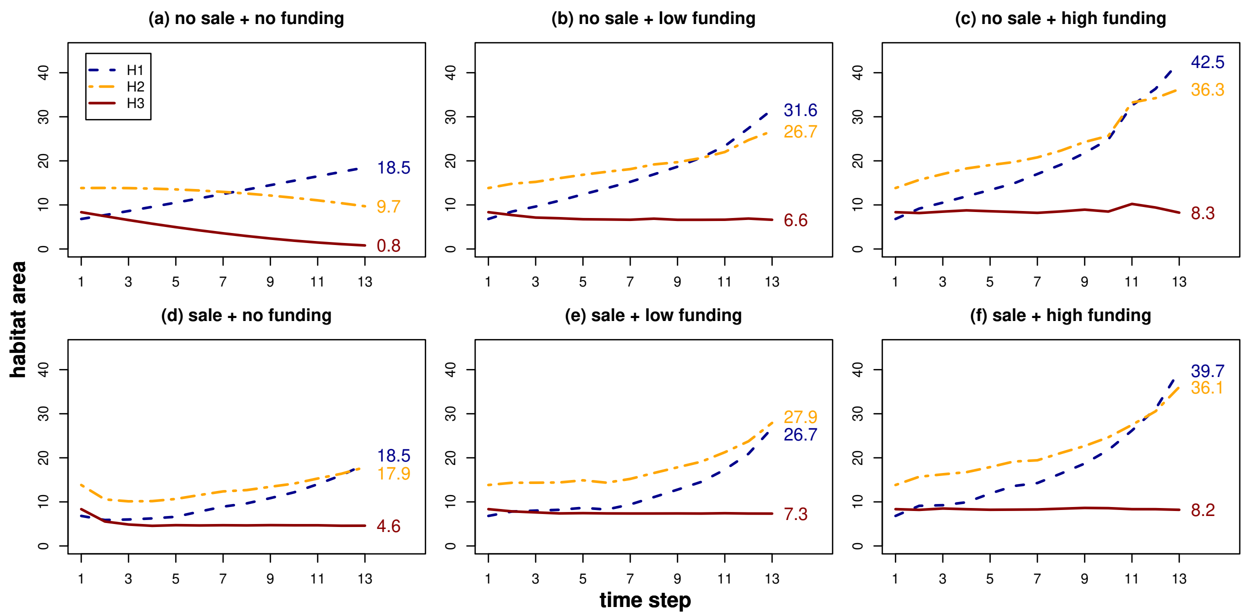


**Figure 4.** Area covered by each habitat type over time for the 'no sale' (a-c) and 'sale' policies and levels of additional funding ranging from none (a, d), low ($k(t) = 50\mu$) (b, e) and high ($k(t) = 100\mu$) (c, f).

### 4.2 'Sale' vs. 'no sale' policy: habitat permanence comparison

Figure 5 shows the share of conservation sites that are maintained throughout the run-time of the model for different funding levels for the 'sale' and 'no sale' policies. In the 'no sale' policy, 100% of sites are maintained due to the restriction on sales for all funding levels. In the 'sale' policy, permanence is lower than in the 'no sale' policy but increases with the amount of additional funding available from approx. 65% ($k(t) = 0\mu$) to approx. 85% ($k(t) = 100\mu$).

When the main objective of the decision maker is to maximising habitat areas, increasing permanence may only be achieved by increasing the available budget. In order to gain an understanding of the costs of increasing permanence, we examine the level of permanence that is achieved when moving from one funding level to the next: Figure 5 shows that the marginal cost of increasing the permanence of conserved sites decreases with increasing funding level.

However, given climatic changes, maintaining a stable reserve network does not necessarily lead to habitat permanence, as climatic changes themselves may lead to a loss of habitat even when the sites are maintained (Lewis and Polasky, 2018). We therefore also consider the level of permanence

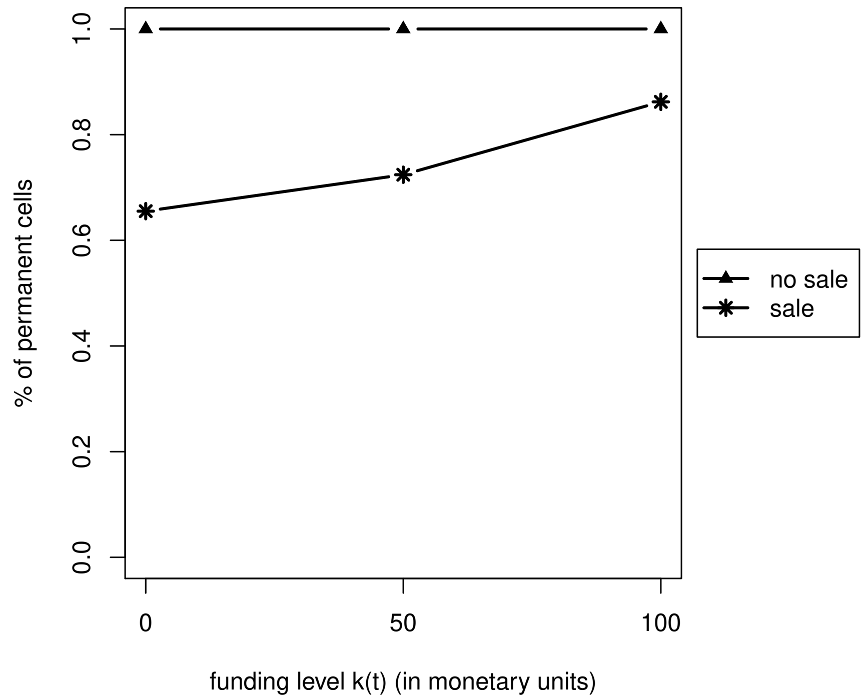


**Figure 5.** Habitat permanence measured as the % area of the original reserve network maintained in all time steps depending on the level of funding.

achieved for each habitat type – measured as the % of the area covered initially by habitat type $H_k$ that is maintained throughout the run-time of the model (Figure 6).

Considering the 'no sale' policy, Figure 6 shows that even if sales are not permitted, 100% of initial habitat areas can be maintained over time only for $H_1$ (the expanding habitat type). For $H_2$ (the shifting habitat type), even under 'no sale' only 70% of initial habitat areas can be maintained under climate change, while for $H_3$ (the contracting habitat type), only 10% of initial habitat areas can be maintained due to changing climatic conditions. Hence, climate change causes habitat turnover even in a static reserve network.

Comparing the 'sale' and 'no sale' policies, it can be seen that habitat permanence tends to be lower under the 'sale' policy. However, two effects can be observed: (1) habitat permanence increases under the 'sale' policy with increasing levels of funding and (2) the difference between the 'sale' and 'no sale' policies is smallest for the habitat type that becomes most threatened, $H_3$. Sites that contain $H_3$ are therefore unlikely to be sold even if they could be. This means that allowing for

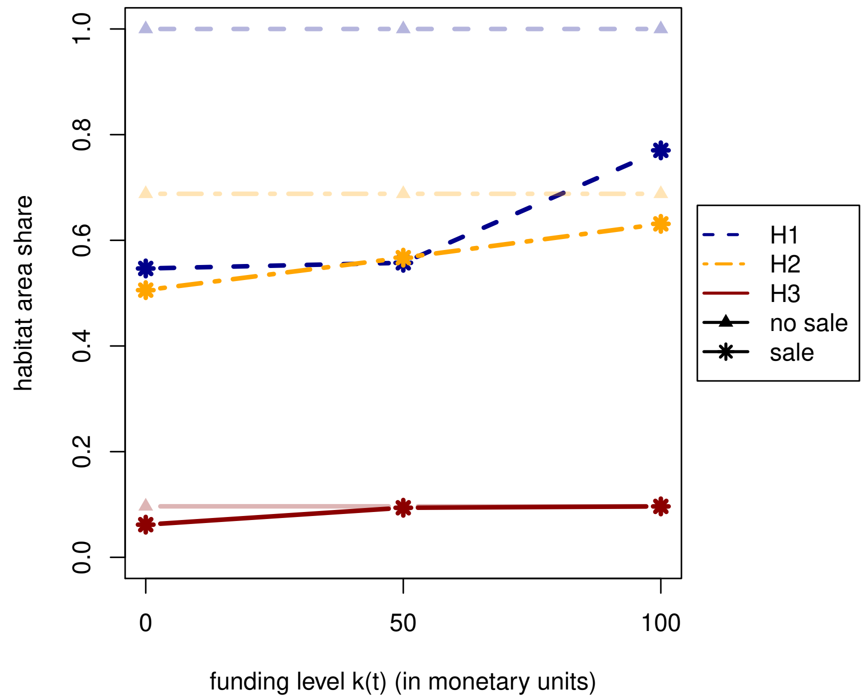


**Figure 6.** Habitat permanence measured as the % of the original habitat area maintained in all time steps depending on the level of funding.

sale tends to decrease habitat permanence when compared to the 'no-sale' case, but mainly for the expanding habitat type.

Considering the costs of increasing permanence, we observe that the marginal costs of increasing habitat permanence decrease for $H_1$ (the expanding habitat type), are relatively constant for $H_2$ (the shifting habitat type), and increase for $H_3$ (the contracting habitat type). While the difference in permanence between the 'sale' and 'no sale' policies is quite low for $H_1$, it is very high for $H_3$: increasing marginal costs are hence observed as the maximum is approached.

## 5 DISCUSSION AND CONCLUSION

Under climate change, the comparative advantage of potential reserve sites to "produce" habitat may change. To maintain cost-effectiveness, reserve networks hence need to be adapted. However, policy instruments may limit the flexibility necessary to adapt to climate change. We analyse two versions of land purchase in order to assess their suitability for the climate adaptation problem in biodiversity conservation: a 'no sale' policy (representing an irreversible investment) and a 'sale' policy (representing a partially reversible investment). We assess the cost-effectiveness (in terms of habitat area) of both policy options as well as their degree of habitat turnover. We use a CEE model to analyse the trade-off between the 'sale' and the 'no sale' policies for different funding levels for a conceptual case study. Finally, we examine the cost of increasing habitat permanence under climate change. We would like to highlight two key results.

First, our results provide some understanding of the costs of maintaining the RD-problem as an irreversible investment by not allowing for the sale of reserve sites given changing climatic conditions. When no additional capital is available, allowing for sale is the only option of adapting the reserve network. Consequently, the improvement achieved by allowing for sales increases the area covered by the most threatened habitat type by a factor of almost five. When additional funding ('low funding' case) is available, the 'sale' option still increases the outcome for the most threatened habitat type, although to a lesser extent. However, in the 'high funding' case, the advantage of the 'sale' option ceases. Previous research has suggested that allowing the sale of reserve sites may improve cost-effectiveness under the dynamic conditions of climate change (Alagador et al., 2014, 2016). However, a trade-off exists with the general negative ecological consequences of selling due to habitat turnover (Lennox et al., 2017). Previous research has suggested that this trade-off may be reduced by tying the 'sale' option to restrictions on future land use (Hardy et al., 2018), and that temporary protection may be particularly valuable for early-successional habitats (Ranius et al., 2022). Our research suggests that two additional important factors influencing this trade-off are whether, and to what extent, other sources of funding are available for adapting the reserve network, and how climate change influences the relative occurrence of the habitat type in question: the benefits of 'sale' are particularly high when little funding is available for the adaptation and when aiming to conserve habitat types that become increasingly threatened due to climate change.

Second, we find that habitat turnover occurs even if the reserve network remains static as changing climatic conditions cause changes in the distribution of habitats within the static reserve network. When comparing habitat permanence between the 'sale' and the 'no sale' policies, we see that the 'no sale' policy mainly increases habitat permanence of $H_1$ (the expanding habitat type), while the difference in habitat permanence of $H_3$ (the contracting habitat type) between the 'sale' and the 'no sale' policies is very small. This is due to the increasing scarcity of this habitat type, which drives the selection of new reserve sites and, to a large extent, prevents the sale of sites which are particularly valuable for this habitat type.

Overall, we therefore identify a new trade-off between the ’sale’ and ’no sale’ policies: ’sale’ provides advantages for habitat types that become increasingly threatened, especially for low levels of additional funding, as ’sale’ then provides an important funding option to adapt the reserve network to changing climatic conditions. ’No sale’ on the other hand improves habitat permanence mainly for the expanding habitat type, while only little ”permanence” is lost under ’sale’ for the most threatened habitat type. Previous conceptual research has identified the trade-off between permanence and flexibility of conservation under climate change (Gerling and Wätzold, 2021). This research is, to the best of our knowledge, the first to identify this trade-off through modelling. This allowed us to gain new insights on how this trade-off plays out for different habitat types. Considering this information may hence lead to new evaluations of whether or not to allow for sale: our research provides some indication that the trade-off does not affect all habitat types equally, but may rather manifest itself in a trade-off between permanence of expanding habitat types vs. overall outcomes for contracting habitat types. Considering climate change-adapted conservation strategies, Gerling and Wätzold (2021) have suggested that spatial flexibility is particularly important for enabling a species’ migration towards newly suitable areas, while maintaining permanence is particularly important for conserving so-called climate refugia, i.e. areas in which climatic conditions remain relatively stable despite climate change. Our research suggests that allowing for sale may hence be a viable option for enabling migration.

Previous economic research has mainly focused on the advantages of flexibility under uncertainty (Arrow and Fisher, 1974; Miller and Lad, 1984; Hanemann, 1989; Albers, 1996), also considering the problem of biodiversity conservation under uncertainty (Kassar and Lasserre, 2004; Leroux et al., 2009; Mezey et al., 2010; Lennox et al., 2017; Lewis and Polasky, 2018; Drechsler, 2020). In the context of conservation under climate change, the possibility of selling may hence provide value as the conservation agency does not have to commit initially to irreversible investments (Ando and Hannah, 2011). However, climate change adds another, new dimension to the trade-off faced by a decision-maker of whether or not to allow selling reserve sites even if there was no uncertainty about future climatic conditions (Strange et al., 2006; Gerling and Wätzold, 2021; Schöttker and Wätzold, 2022): selling causes ecological and transaction costs, but also allows for an adaptation of the reserve network by adding increasingly cost-effective sites and eliminating sites which are increasingly less cost-effective. Apart from climate change uncertainty, changes in the comparative advantage of some sites over others hence provide another argument for increasing flexibility. This latter argument has so far rarely been considered. With this article, we hence go beyond previous research by addressing the potential advantages and trade-offs of increasing flexibility due to changes in comparative advantages.

As in any model, we had to make some assumptions to simplify reality. First, we assume that the habitat is generated instantly once a grid cell is conserved. Considering the time lag between conservation action and outcomes essentially creates a ”conservation credit” (as opposed to an ”extinction debt” when species do not become extinct immediately after a habitat is degraded) (Watts et al., 2020). Including a time lag would reduce the benefits in conservation strategies relying on frequent habitat turnover. Given the conceptual nature of the model, we decided against specifically modelling this aspect: the size of the time lag may vary between years and centuries or even millennia (Watts et al., 2020) and depend largely on the habitat type in question (Drechsler and Hartig, 2011; Wilson et al., 2011; Possingham et al., 2015), the initial conditions of the site to be restored (Wilson et al., 2011), the connectivity to the existing reserve network (Watts et al., 2020) and the dispersal ability of the species inhabiting the chosen habitat type (Watts et al., 2020). Due to these varied interactions we decided against modelling this aspect and refer the interested reader to previous research on the topic (Drechsler and Hartig, 2011; Possingham et al., 2015). Similarly, the creation of a habitat site may not necessarily translate to all expected species actually inhabiting that site - if the aim is to conserve a specific species, species-based approaches rather than a habitat-based approach may therefore be more suitable (Simpson et al., 2022).

Second, the economic model contains some simplifications. We assume that the prices of the grid cells remain constant. Under climate change, opportunity costs of land parcels will likely be affected in a spatially heterogeneous manner (Schöttker and Wätzold, 2022; Gerling et al., 2022a). Regarding conservation in agricultural landscapes, for example, some areas may become more suitable for agricultural activity (for example areas in higher altitudes), while others may become less suitable (for example areas suffering from increasing droughts), which may lead to opposing developments of opportunity costs (Ray et al., 2019; Lachaud et al., 2021). If climate change leads to a relative decrease (increase) in conservation costs of newly (formerly) cost-effective sites, the cost-effectiveness of the static reserve network is further reduced (increased) in comparison to the case of static opportunity costs. Additionally, changes in opportunity costs may influence the degree of reversibility when sales are allowed: an increase (decrease) in opportunity costs due to climate change of formerly cost-effective sites in combination with a decrease (increase) in costs of newly cost-effective sites may decrease (increase) the costs of reversibility, as the selling price exceeds (is lower than) the price at the time of purchase. However, we decided to ignore these aspects as the changes to opportunity costs depend largely on which area is considered. Future research based on specific case study areas or on conceptual models investigating the interactions between the relevant variables may include these aspects in a similar model.

The adaptation of the RD-problem applied in this article is able to assess the cost-effectiveness of different policy scenarios for climate adaptation of biodiversity conservation. A similar model may be used in future research to address other questions of conservation under climate change. In particular, we would like to suggest the following two topics for future research:

First, in our model we consider two extreme cases of the ’sale’ and ’no sale’ policies. Future research could examine the outcomes of medium levels of flexibility - e.g. in conservation easements or ’purchase, protect, resale’ programmes (Hardy et al., 2018), in which land may be sold with restrictions on future land use. This may be a compromise between increasing flexibility and maintaining habitat permanence under climate change, and may hence be more acceptable for policy makers. Therefore, this option may be particularly relevant when parameterising the model to a specific case study.

Second, we explicitly do not consider uncertainty in order to examine the value of flexibility that arises additionally to the value of flexibility under uncertainty. Nonetheless, we acknowledge that considering uncertainty under changing climatic conditions is important and that our model may be adapted to build on the previous literature in this field. In particular, we have assumed that the conservation agency has perfect foresight and is hence able to determine the optimal spatial allocations of reserve sites over time. In the case of imperfect foresight, a seemingly optimal decision at present may however turn out to be suboptimal in hindsight in the future (Drechsler and Wätzold, 2020). Delaying an irreversible investment decision may hence provide quasi-option value (Arrow and Fisher, 1974). The role of this quasi-option value for optimal climate adaptation pathways in the RD-problem may hence be analysed (cp. Miller and Lad (1984), Albers (1996), Leroux et al. (2009), Brunette et al. (2014), Brunette et al. (2020)). In particular, one may consider that on the other hand, securing sites early when there is a threat of irreversible land conversion (such as housing development) (Costello and Polasky, 2004; Strange et al., 2006) increases the value of investing early rather than later. We believe that exploring this trade-off is particularly interesting when considering the impact of climate change, as it further increases uncertainty of ecological outcomes and costs and thus increases the potential quasi-option value.

Given the rapid loss of global biodiversity (Dasgupta, 2021) and the need to adapt existing reserve networks to climate change (Pyke and Fischer, 2005; Fung et al., 2017; Graham et al., 2019; Lawler et al., 2020), we believe that further (economic) research on how to design policy instruments of biodiversity conservation for the climate adaptation problem will provide valuable information to conserve biodiversity cost-effectively in the future.

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# SUPPLEMENTARY MATERIAL

## A NEIGHBOURHOOD

In the presented model, the conservation agency is limited in the selection of grid cells to be purchased by the proximity of the grid cells to the existing reserve network at any time $t$. We assume that a grid cell only provides a contribution to the reserve network if it is located within a certain distance $d$ defined by the combined Moore neighbourhood around already conserved grid cells. Any grid cells $M_{ij}$ which are located within this distance $d$ around current reserve site $\{i, j\}$ are those that are part of the combined Moore neighbourhood at time $t$. Those cells are shaded yellow in Figure A.1.

This assumption is reasonable as isolated habitats (i.e. grid cells too far away from the reserve network) might potentially provide habitat, but this may not be realised if the sites are not accessible by any target species relying on the potentially provided habitat type, as they lie beyond the species' dispersal abilities (Schöttker and Wätzold, 2022; Hily et al., 2017). Hence, adding grid cells beyond a combined Moore neighbourhood would be ecologically ineffective and not cost-effective per se and is thus assumed impossible in our model.

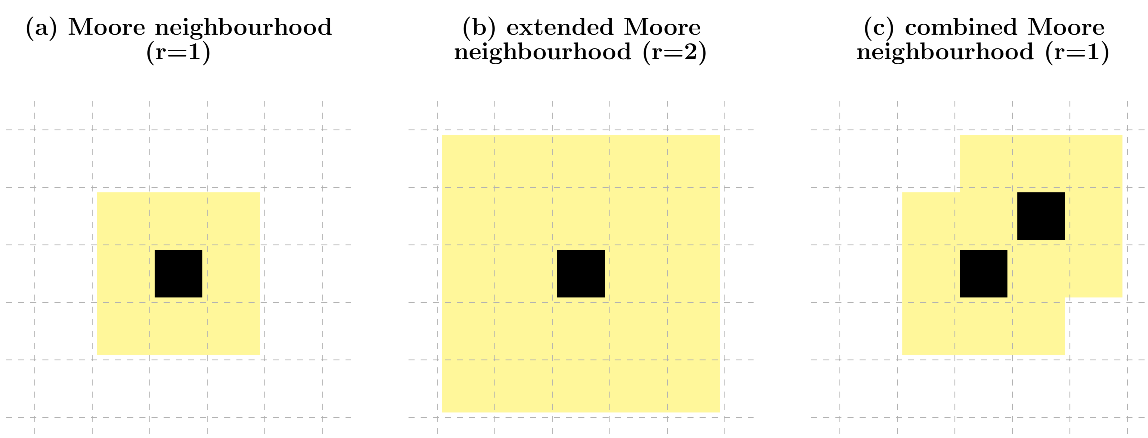


**Figure A.1.** Illustration of the (a) Moore neighbourhood ($d = 1$) of a grid cell, (b) the extended Moore neighbourhood ($d = 2$), and (c) the combined Moore neighbourhood of two cells ($d = 1$).