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

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## ABSTRACT

Climate change causes range shifts of species and habitats, thus making existing reserve networks less suitable in the future. 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. In principle, reserve networks may be adapted to climate change in two ways: by providing additional funds and/or allowing for the sale of sites to liquidate funds for new purchases. However, due to negative ecological consequences, selling is often regulated, thus rendering the optimal reserve design a problem of irreversible investment decisions. Respectively, allowing for sale may be interpreted as an investment with costly reversibility, as transaction costs do not allow for full recovery of the initial investment. Here, we assess the gains in terms of cost-effectiveness achieved when allowing for sale as well as the costs of this flexibility in terms of habitat turnover given climate change-induced changes in comparative advantages. To do so, we develop a conceptual climate-ecological-economic model to find the optimal time series for the reserve design problem under changing climatic conditions and different policy scenarios. These scenarios differ in the size of additional funds for climate adaptations and whether selling is allowed. Our results show that the advantage of selling 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 to adapt biodiversity conservation to climate change: 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; irreversible investment; investment with costly reversibility; selling reserve sites

# 1 INTRODUCTION

Existing nature reserves are unlikely to protect their target species in the future unless they are adequately adapted to climate change (Heller and Zavaleta, 2009; Vincent et al., 2019). This is due to shifts in species' ranges and the distribution of potential habitats caused by changing climatic conditions (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 existing reserves under climate change to maintain chosen habitat types in chosen case study areas (Pyke and Fischer, 2005; Fung et al., 2017; Graham et al., 2019; Lawler et al., 2020). However, most current research presents the additional, optimal reserve sites of a case study area necessary at some chosen point in the future. This does not consider that conservation activities are typically 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. (2022) examine changes in the cost-effective conservation measures of an agri-environment scheme over time due to climate change. Here, we examine land purchase by a conservation agency to create reserves as a typical policy instrument for biodiversity conservation (Armsworth et al., 2006; McDonald-Madden et al., 2008; Schöttker et al., 2016; Hardy et al., 2018) and assess whether a novel design of the instrument that provides spatial flexibility for climate adaptation may improve cost-effectiveness. We hence address a key issue of the climate adaptation problem for biodiversity conservation - spatial flexibility - and the implications this has for one of the most prominent policy instruments for biodiversity conservation, land purchase.

Reserves may in principle be adapted to climatic changes by adding new sites to the reserve network from additional funds or by selling existing sites and using the recovered funds for the purchase of new sites. From an economic perspective, the purchase of reserve sites may be analysed by considering purchases as investments. In investment theory, investments may be distinguished by their degree of reversibility, ranging from fully reversible investments (which imply full recoverability of initial investment costs (Davis and Cairns, 2017)) to irreversible investments (Arrow, 1968; Pindyck, 1988). 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). 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). On the other hand, 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).

However, both adaptation pathways face important challenges: First, conservation funds are scarce and may not be large enough to expand the existing reserve network sufficiently. Considering the option of selling, negative ecological consequences due to habitat turnover (Ando and Hannah, 2011; Lennox et al., 2017; Gerling and Wätzold, 2021) and transaction costs such as taxes and the search for suitable sites for selling and buying (Schöttker and Wätzold, 2018) are important disadvantages of selling existing reserve sites. For these reasons, selling reserve sites is often not permitted in practice (Fuller et al., 2010; Lennox et al., 2017). Against this background, the question of whether or not to allow selling reserve sites can therefore be interpreted as 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).

Regarding the economic literature, previous literature has focused on the advantages of increasing flexibility in the case of 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, 2020a). 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, and whether (and under which circumstances) climate change may justify the option of selling remains an open question.

Recent research provides some evidence that the advantages of selling may outweigh the costs under changing climatic conditions even under the assumption of perfect information, 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 assess the gains in cost-effectiveness achieved by the ’sale’ option as well as the resulting losses in habitat permanence by comparing it to the ’no sale’ option. 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.

Due to the complexities inherent in decisions taking into account both spatially and temporally dynamic changes to ecological and economic variables, modelling has proved to be a useful tool for understanding the relationships between different system components (Drechsler, 2020c; Grimm et al., 2020). Models to understand cost-effective reserve design developed in the last decades rely mainly on four approaches:

(1) **Case study- and species-specific ecological-economic models** (Johst et al., 2002; Polasky et al., 2008; Wätzold et al., 2016; Drechsler, 2020c). These models are typically based on more or less complex ecological and economic models and consider case study landscapes with spatial differences in conservation costs and benefits. Cost-effective conservation sites are chosen via criteria such as the benefit-cost ratio (Duke et al., 2014). These types of models allow mechanistic or process-based modelling of the species, where the different physiological processes of the species are modelled rather than relying on species distribution models with limited relevance when extrapolating to, for example, new climatic conditions (see Evans et al. (2015) for a review on this and Gerling et al. (2022) for an example). Furthermore, aspects such as the impact of climate change (Arafeh-Dalmau et al., 2020; Drechsler, 2020b; Gerling et al., 2022) and climate change-induced range shifts (Midgley et al., 2010) may be included.

(2) **Conceptual ecological-economic models targeting species conservation** (Drechsler et al., 2022). Cost-effectiveness again is approached with heuristics such as the benefit-cost ratio. In contrast to the former, these models are not case study-specific and may be used to understand more general system interactions. Additional complexities such as metapopulation dynamics (Costanza and Voinov, 2001; Drechsler and Johst, 2010; Schöttker et al., 2016; Drechsler and Johst, 2017) and the impact of climate change (Schöttker and Wätzold, 2022) are therefore included more commonly. Considering uncertainty under climate change, Drechsler (2020a) examines the value of increasing flexibility and robustness in a two-period model.

(3) **The RD-problem in the field of optimization, applied to specific case-studies** (Ando et al., 1998; Polasky et al., 2001; Hamaide et al., 2014). These studies usually consider both costs and conservation benefits in order to find the optimal reserve network. Cost-effectiveness in these studies is usually formulated as two archetypal problems: the Species Set Covering Problem (SSCP) and the Maximal Species Covering Problem (MSCP). In both cases, a landscape consists of potential sites containing different species. Regarding the SSCP, the problem is to find which sites to protect

to conserve a set of desired species whilst minimizing costs (Moore et al., 2003; Jafari and Hearne, 2013; Snyder and Haight, 2016). Regarding the MSCP, the number of species to be protected is maximised given a certain budget constraint (Church et al., 1996; Polasky et al., 2005). Previous research has focused on connectivity (Önal and Briers, 2003; Önal and Briers, 2005, 2006) and the adaptation of existing reserve networks (van Langevelde et al., 2002). Recent work in this field adds the temporal dimension in multi-period RD-problems (Jafari et al., 2017). Regarding the impact of climate change, Dissanayake et al. (2012) develop an RD-problem considering the option of species relocation while Alagador and Cerdeira (2020) examine optimal migration corridors.

(4) **The RD-problem in the field of optimization at a conceptual level** (Dissanayake and Önal, 2011; Jafari and Hearne, 2013). These studies are also formulated in terms of the SSCP and MSCP. Often, these studies examine the impact of certain variables on the the optimal solution conceptually, such as the value of information (Polasky and Solow, 2001) or temporal changes in costs (Dissanayake and Önal, 2011). Other research in this field focuses on novel optimisation procedures (Alagador and Cerdeira, 2021), such as explicitly considering the neighbourhood relations between sites in an adaptation of the RD-problem called the ”reserve network design problem” (Jafari and Hearne, 2013).

In this paper, we develop a climate-ecological-economic (CEE) model to investigate the suitability of irreversible conservation investments and investments that are reversible at a cost under climate change. We go beyond previous research which has mainly focused on the advantages of flexibility under uncertainty, and examine whether there is any value in flexibility even when the conservation planner has complete information, thus focusing on the value of flexibility due to changes in comparative advantages. We explicitly consider the trade-off that emerges as increasing flexibility may also increase habitat turnover. We apply the model to the example of 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 outcome when selling reserve sites is allowed to the case in which selling is not allowed. We consider different budget constraints to examine whether the size of the budget has an influence on the comparison. Finally, we acknowledge that habitat permanence is considered important for ecological reasons and 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 the problem of how to adapt biodiversity conservation to the challenges of climate change.

# 2 DECISION PROBLEM: CONCEPTUAL CONSIDERATIONS

## 2.1 Multi-objective optimisation

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). 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 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 use the SSCP or MSCP and 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.

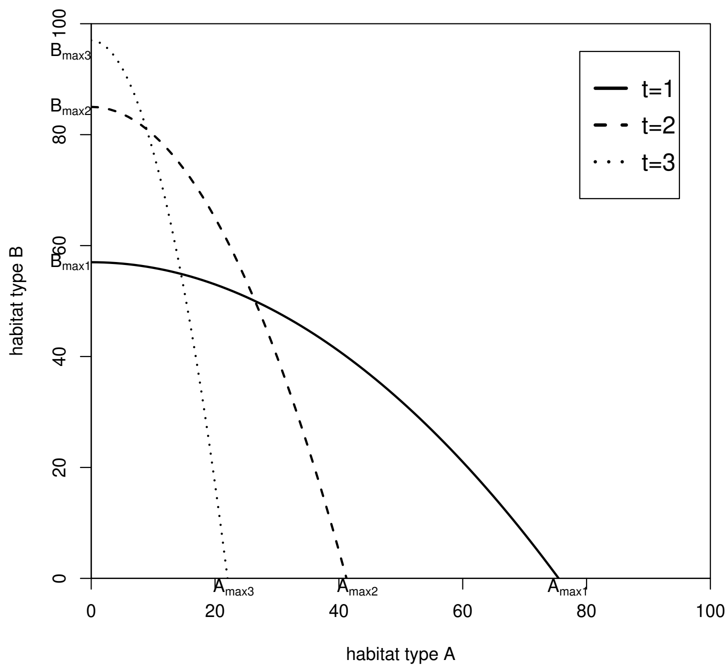


**Figure 1.** Hypothetical changes to production possibility frontiers at time steps $t \in \{1, 2, 3\}$ for two habitat types A and B.

The SSCP and MSCP may not capture these dynamics adequately. In the SSCP, the set of species to conserve at minimum costs may no longer be viable if a species becomes extinct under climate change. When considering certain minimum threshold values in order to avoid very small habitat areas under the MSCP, 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.

In order to address these challenges, we develop an optimisation procedure that considers the changes in spatial distributions of habitat types and in their relative occurrence. To do so, we consider the maximum value that may be achieved for each habitat type in each time step, representing the points where the PPF touches the axes. Based on this information, we apply a goal programming approach in order to adapt the *maximin* approach to changing climatic conditions and aim to maximise the minimum values of each habitat type over time.

# 3 MATERIALS AND METHODS

## 3.1 Model setup

We first solve a static optimisation problem by applying a *maximin* approach subject to a budget constraint. This optimal reserve network is then used as the starting point as we investigate the consequences of climate change for different, stylised habitat types. We again apply a *maximin* approach subject to a budget constraint to generate the optimal dynamic reserve network. The modelling procedure explicitly considers dynamic changes to the scarcity and spatial distribution of different habitat types under climate change and calculates a time series of optimal habitat networks within these dynamic conditions.

We then apply the model to a hypothetical case study to gain an understanding of the value of selling of reserve sites under climate change and the negative consequences in terms of habitat turnover that selling may cause. Here, we consider different policy scenarios defined by whether or not selling is allowed. Additionally, we consider different budget constraints to see whether the size of the budget has an impact on the outcomes.

We utilize the JuMP modelling language (Dunning et al., 2017) in the Julia programming environment (Bezanson et al., 2017) to set up the CEE model, and the Gurobi optimiser (Gurobi Optimization, LLC, 2021) to solve the optimisation for a global optimum. Standard packages of the

R software are used for processing and visualization of results (R Core Team, 2018).

## 3.2 Optimisation procedure

### *3.2.1 Formulation of the initial optimisation problem*

We consider $K$ habitat types on a landscape with multiple sites. We assume that initially, the conservation agency owns a reserve comprising a network of sites that is optimal under current climatic conditions, and that contains all three available habitat types $H_k$. The initial reserve network maximises the conservation outcome under initial climatic conditions given an initial budget constraint $B$. To achieve contiguity of conservation sites within the reserve network, we assume that new sites can only be purchased if they are located within the Moore neighbourhood (Gray, 2003) of a site already in the reserve network (see Supplementary Material C for a more detailed description).

Following the approach of Jafari and Hearne (2013), we represent each site as a node. The budget is initially located at a *source* node outside of the grid. The problem is then regarded as a transshipment problem. Capital flows from the source to a node in the grid and from there to other connected nodes. Each node has a demand for capital equal to its cost and a reward equal to its habitat value. Capital cannot flow through a node without meeting its demand, i.e. without it being purchased. In this way contiguity is ensured while meeting some objective. Table 1 provides an overview of the sets, indices, parameters and variables used in the mathematical formulation of the initial optimisation procedure.

We first formulate the constraints of the problem.

$$\sum_{j \in M_{i+}} x_{ji} - \sum_{j \in M_i} x_{ij} \geq p_i * \sum_{j \in M_{i+}} y_{ji} \qquad \forall i \in N \tag{1}$$

$$\sum_{j \in M_{i+}} y_{ji} \leq 1 \qquad \forall i \in N \tag{2}$$

$$y_{ij} \leq x_{ij} \qquad \forall i \in M_{j+}, \forall j \in N \tag{3}$$

$$x_{ij} \leq B * y_{ij} \qquad \forall i \in M_{j+}, \forall j \in N \tag{4}$$

$$\sum_{i \in N} y_{0i} = 1 \tag{5}$$

$$y_{ij} \in \{0,1\}, \quad x_{ij} \geq 0, \qquad \forall i \in N_+,\ j \in N \tag{6}$$

Constraint 1 represents the flow of capital. The capital flowing into site $i$ must be greater than or equal to the cost of the site plus the capital flowing out of it. Constraint 2 ensures that capital can only flow into a site from one source. This ensures that each site is purchased only once. Constraints 3 and 4 ensures that capital will only flow from $i$ to $j$ if and only if $y_{ij} = 1$, indicating that site $j$ is purchased. Constraint 5 with 3 forces capital to flow from the *source* and to only one site. Thus, we create one single connected reserve network. Constraint 6 provides necessary function rules for $x_{ij}$, $y_{ij}$, $i$ and $j$.

| Symbol | Description |
|---|---|
| $N$ | set of all nodes in the $n \times m$ grid |
| 0 | the *source* node |
| $N_+$ | set of all site nodes plus the *source* node |
| $M_i$ | set of all sites in the Moore neighbourhood of site $i \in N$ |
| $M_{i+}$ | set of all neighbouring sites plus the *source* node, i.e. $M_{i+} = M_i + \{0\}$ |
| $B$ | budget available for purchasing sites |
| $p_i$ | cost of site $i$ |
| $h_{ki}$ | conservation value of site $i$ for habitat $H_k$ |
| $b_i$ | binary variable equal to one if site $i$ is selected, else zero |
| $y_{ij}$ | binary variable equal to one if money flows from site $i$ to site $j$ (indicating site $j$ is selected for purchase), else zero |
| $x_{ij}$ | amount of capital that flows from site $i$ to site $j$ |

**Table 1.** Overview of used sets, indices, variables and parameters in the initial optimisation.

**Objective and solution procedure**

We have a multi-objective problem in that we would like to select sites to maximise the utility value with respect to each habitat type. We deal with this using goal programming. Solving to maximise each habitat type in turn subject to the constraints 1-6, we obtain the goals $g_k$ corresponding to each habitat type $H_k$. Thus:

$$g_k = \max \quad \sum_{j \in N} \sum_{i \in M_{j+}} y_{ij} * h_{kj} \qquad \forall k \in K \tag{7}$$

The goal for each habitat is obtained while ignoring the other habitats. We now attempt to obtain habitat values as close as possible to the goals in a multi-objective setting by minimising $\varepsilon$ (cp. equation 8). Thus we replace the previous objectives and add a new constraint to the previous constraints, as given below.

$$\begin{aligned} &\min \quad \varepsilon \qquad \text{subject to:} \\ &\big(g_k - \sum_{j \in N} \sum_{i \in M_{j+}} y_{ij} * h_{kij}\big)/g_k \leq \varepsilon \quad \forall k \in K \end{aligned} \tag{8}$$

### *3.2.2 Formulation of the dynamic optimisation problem*

We expect the habitat quality of this initial reserve network to deteriorate with time under climate change. In this section we therefore formulate a dynamic optimisation model that allows for adaptation of the initial reserve network through buying (and, under the 'sale' strategy, selling) of sites over $T$ time-periods, each of duration $\tau$ years. The sets, indices, parameters and variables used in the formulation of the mathematical model are given in Tables 2. Note that the notation regarding budget is changed for the dynamic problem as we no longer require the capital flow approach to solve this problem. We also changed notation regarding the reserve site indices to be able to address different reserve sites in the Moore neighbourhood appropriately.

From the initial static optimisation problem we have the values (0 or 1) of $y_{ij0}$, indicating whether or not the respective sites form part of the initial reserve network. The initial capital for the dynamic optimisation is set at $c(0) = k(0)$. The dynamic system is subject to the following constraints.

$$\sum_{i \in N} (1+a) * p_i * b_{it} \leq c(t) \qquad \forall t \in T \tag{9}$$

| Symbol | Description |
|---|---|
| **Sets, Indices** | |
| $N$ | set of all sites, $i \in N$ |
| $M_i$ | set of all sites in the neighbourhood of site $i$ |
| $T$ | set of all time periods, $t \in T$ |
| $K$ | the set of all habitat types, $k \in K$ |
| **Parameters** | |
| $\tau$ | duration of each time period (years) |
| $a$ | transaction cost of buying or selling a site |
| $p_{it}$ | price of property $i$ at time $t$ |
| $h_{kit}$ | utility of habitat type $k$ of site $i$ at time $t$ |
| $r$ | annual interest (discount) rate |
| $c(t)$ | capital available at time $t$ |
| $d(t)$ | additional capital (e.g. from grants or donations) available at time $t$ |
| $\mathbf{M}$ | a large number |
| **Variables** | |
| $y_{it}$ | 1 if site $i$ is owned at time $t$, 0 otherwise |
| $b_{it}$ | 1 if site $i$ is purchased during the period $(t,t+1)$, 0 otherwise |
| $s_{it}$ | 1 if site $i$ is sold during the period $(t,t+1)$, 0 otherwise |

**Table 2.** Overview of used sets, indices, variables and parameters in the dynamic optimisation.

$$
\begin{aligned}
c(t+1) = {} & (1+r)^{\tau} * c(t) + d(t) + (1+r)^{0.5\tau} * \\
& \sum_{i \in N} (1-a) * p_i * s_{it} - (1+a) * p_i * b_{it} \quad \forall t \in T
\end{aligned} \tag{10}
$$

$$
y_{it+1} = y_{it} + b_{it} - s_{it} \qquad \forall i \in N, \forall t \in T \tag{11}
$$

$$
b_{it} \leq \sum_{l \in M_i} (y_{lt} - s_{lt}) \qquad \forall t \in T \tag{12}
$$

$$
b_{it} \leq 1 - y_{it} \qquad \forall i \in N, \forall t \in T \tag{13}
$$

$$
\mathbf{M}(1 - s_{it}) \geq \sum_{l \in M_i} y_{lt} - 1 \qquad \forall t \in T \tag{14}
$$

Constraint 9 ensures that the cost of purchases in any time period cannot exceed the capital available at that time. The cost of purchase is made up of the price of a cell $p_i$ and transaction costs $a$. Transaction costs are measured as a fraction of the price of the site $p_i$. The price of each cell is randomly drawn from a uniform distribution between 10 and 60. We assume prices to differ as opportunity costs of conservation typically differ between different conservation areas. Furthermore, we assume prices are spatially independent and remain constant over time. $b_{it}$ is a dummy variable indicating whether or not site $i$ is purchased in time $t$ or not.

Constraint 10 keeps track of the flow of capital. The available capital is made up of three parts: (1) any remaining budget from the previous period including interest payments, (2) any payment $k(t)$ received in that period and (3) if the agency has sold any sites, funds from selling cells $((1-a)*p_i)$ net of transactions costs $a$ (measured as a fraction of the original price of that site $p_i$) are also available as capital for the next time period. Note that $s_{it}$ is a dummy variable indicating whether or not site $i$ has been sold in time $t$ or not. Buying and selling occurs throughout each period but for simplicity we assume that all transactions occur halfway through the period and thus incur corresponding interest.

Constraint 11 updates the sites owned after sales and purchases. To maintain connectivity, constraint 12 will only allow a site to be purchased if there will be at least one other property in its Moore neighbourhood. Constraint 13 ensures that we do not buy a site already owned. Constraint 14 is introduced to reduce breaking up clusters. Only sites that have at most one owned site in its neighbourhood are allowed to be sold. A standard 'big M' formulation is used here to ensure there is no unwanted constraint placed on the binary variables on the right hand side of the constraint in the event that site $i$ is not to be sold. An appropriate value for $\mathbf{M}$ is the smallest number such that no site has more than $\mathbf{M}$ neighbours.

Constraints 12 and 14 together encourage rather than guarantee contiguity.

**Objectives and solution procedure**

We aim to maximise the minimum values of each habitat type at any time $t$. As we consider $K$ habitat types, we have a multi-objective problem which we formulate using a goal programming approach. We begin by solving the following $K$ problems subject to the constraints 9-14 given above.

For $\forall k \in K$ solve:

$$\Gamma_k = \max\ \theta \tag{15}$$

$$\text{subject to: } \sum_{i \in N} h_{kit} * y_{it} \geq \theta \qquad \forall t \in T \tag{16}$$

Having obtained the goals, $\Gamma_k$, we proceed to the multi-objective problem where we aim to minimise the deviations from the goals. Thus, still subject to the constraints 9-14, we have additional constraint 18 together with the objective 17 as given below.

$$\min \quad \varepsilon \tag{17}$$

$$\text{subject to: } \big(\Gamma_k - \sum_{i \in N} h_{kit} * y_{it}\big)/\Gamma_k \leq \varepsilon \qquad \forall t \in T, \quad \forall k \in K \tag{18}$$

The solution to this last problem will yield the sites $i$ that form part of the reserve at each time $t$ as well as the sites that are to be purchased or sold at each time $t$.

## 3.3 Illustrative case study

### *3.3.1 Modelling of the landscape, habitat types and climate change*

To gain an understanding of the value of selling of reserve sites under climate change, we apply the model to a conceptual case study. The landscape in our conceptual case study consists of a grid of $N = 10 * 20 = 200$ equally sized cells. In this landscape, three different habitat types exist ($H_1$, $H_2$, $H_3$), i.e. $K$=3. Each grid cell has a specific utility value for each of the habitat types. One could imagine this as a landscape consisting of different altitudes: each grid cell has a cell-specific elevation level $elev_i$. The elevation level $elev_i$ is assigned in a way that the landscape features three different regions, i.e. a valley, plains of medium elevation, and a mountain (compare Fig. 2, and see Supplementary Material A and Fig. A.1 for details on the construction of the landscape). While some habitat types are more likely to occur in the valley, others are more likely to occur on the mountain.

When a grid cell is conserved, the effective habitat area generated for the different habitat types is given by their respective utilities $h_{kit}$ (see Supplementary Material B for details on the underlying functional relationship). Generally, each region – valley, plains, and mountain – provides ideal conditions for one of the three habitat types, while only providing sub-optimal conditions for the other habitat types. $H_1$ 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.

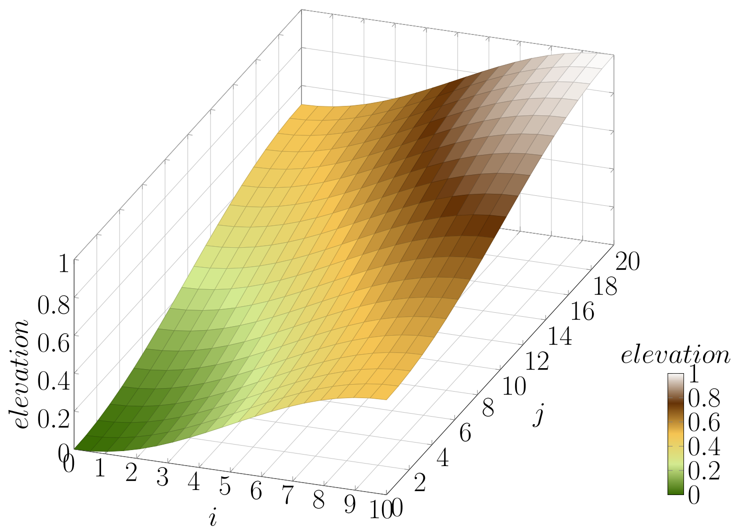


**Figure 2.** Landscape grid and grid cells, coloured by elevation level visualizing the topography of the landscape.

In order to consider changing climatic conditions, the utility $h_{kit}$ is time-dependent. Climate change is hence represented implicitly by the variable $t \in [1, T]$, which is the time step of the model simulation. Each time step $t$ represents a five-year period. Overall, we consider $T$=13 time steps, where $t = 1$ represents the initial optimisation problem. This implies that in the dynamic optimisation, we consider a period of 60 years. Rather than modelling climate change explicitly, e.g. through changes in precipitation or temperature on a grid cell level, we hence model it implicitly by assuming that the climatic changes cause the suitability of each grid cell $i$ for habitat type $H_k$ to change.

Importantly, climate change impacts each habitat type differently: 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. We have chosen these patterns of spatial shifts as they represent typical movements observed in reality: as climatic factors change – such as increasing temperatures in formerly cooler, high-altitude areas – the species' ranges and habitat types move uphill towards areas more suitable under the changed conditions, while the mountainous habitat types are increasingly threatened due to increasing competition and unsuitable climatic conditions (see for example Lamprecht et al. (2018)).

Figure 3 illustrates the suitability of each habitat for all elevation levels for time steps $t = \{1,5,9,13\}$.

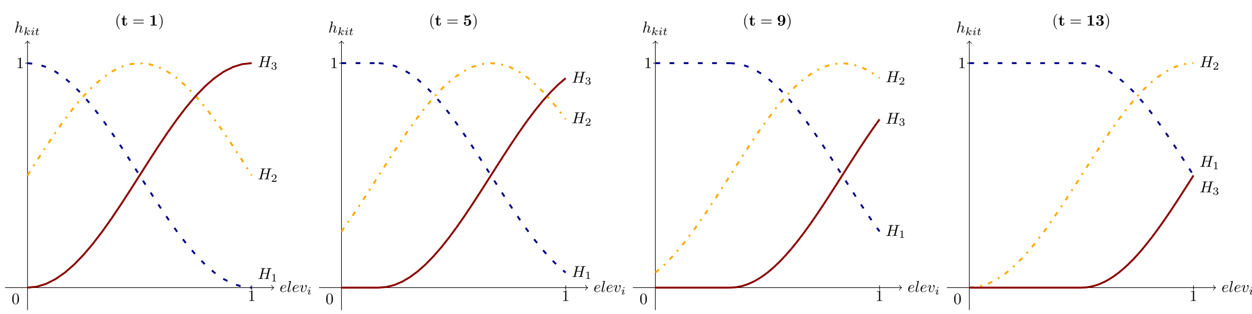


**Figure 3.** Utility level $h_{kit}$ of a cell $i$ at time steps $t \in \{1,5,9,13\}$ for all three habitat types $k \in \{1,2,3\}$.

We assume there is no time lag between the time when a grid cell is conserved and the time when the habitat of that grid cell is generated, i.e. as soon as conserving grid cell $i$, habitat types $H_k$ are present according to their utilities $h_{kit}$. As any grid cells that are not conserved do not provide any habitat, the conserved grid cells represent 'islands' of habitat surrounded by land of no ecological value with respect to the modeled habitat types.

### 3.3.2 Policy scenarios

In order to gain an understanding on whether allowing the conservation agency to sell existing reserve sites under climate change provides any value due to changes in comparative advantages, we consider two general policy strategies - ’sale’ and ’no sale’ - and compare the development of the values achieved for the three habitat types over the 60-year period.

The initial reserve network is generated with an initial budget of $500\mu$ (throughout this section we use $\mu$ to indicate monetary units), representing approximately 7% of the total value of all sites in the landscape. Considering the regular payments $k(t)$, we consider 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 additional budget $k(t)$ available to adapt the reserve network in every time step $t \in \{1,...,T\}$ to realise the reserve network adaptation in the dynamic optimisation. In the ’low funding’ case we assume that the agency receives $50\mu$ during each five-year period (i.e. $k(t) = 50\ \forall t$, see equation 10). In the ’high funding’ case the regular payments are increased to $100\mu$.

# 4 RESULTS

## 4.1 ’Sale’ vs. ’no sale’ policy

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

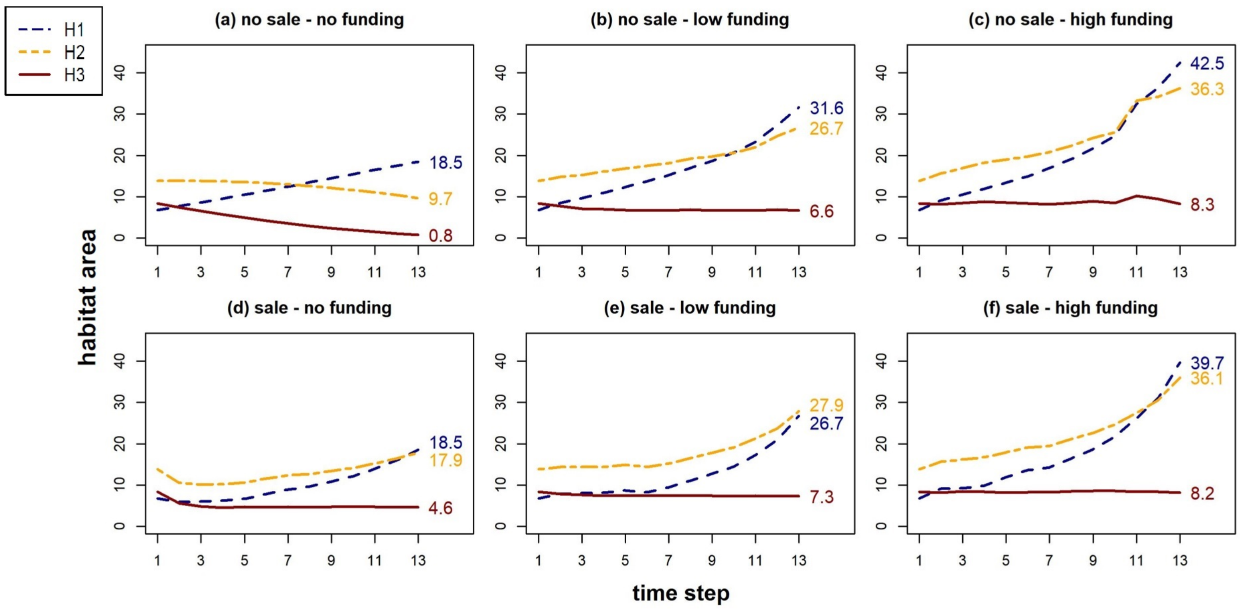


**Figure 4.** Area covered by each habitat type over time for the 'no sale' (a-c) and 'sale' policies and levels of additional funding ranging from none (a, d), low ($k(t) = 50$) (b, e) and high ($k(t) = 100$) (c, f).

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.

## 4.2 Cost of increasing (habitat) permanence

Habitat permanence has a certain value for ecological reasons. However, when the main objective of the decision maker is to maximise the minimum area covered by all habitat types, 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 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,

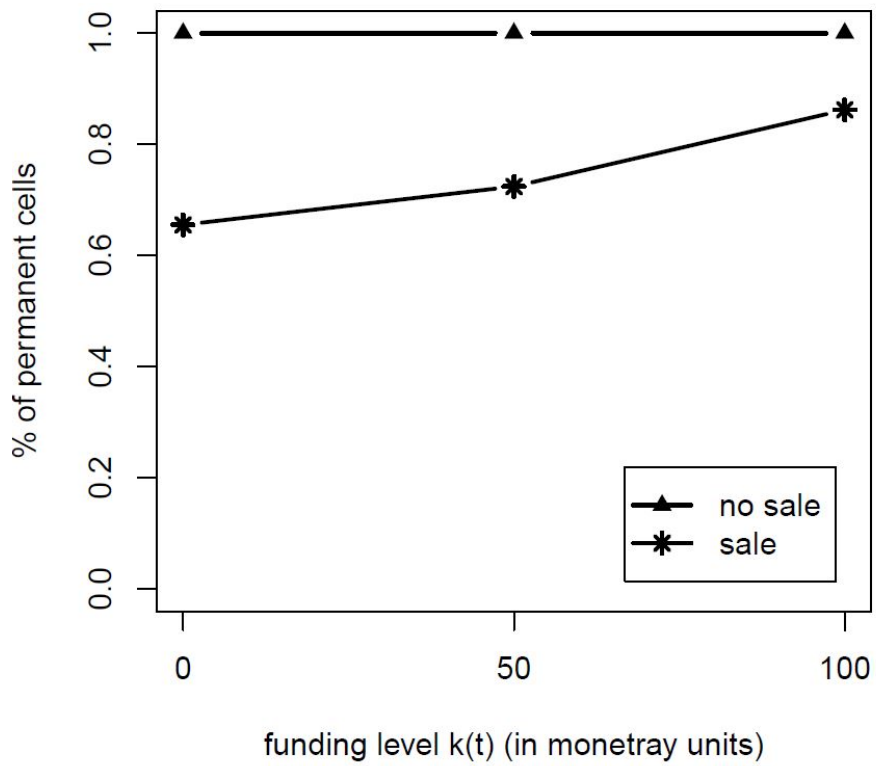


**Figure 5.** Habitat permanence measured as the % area of the original reserve network maintained in all time steps depending on the level of funding.

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% ($k(t) = 100\mu$). 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 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

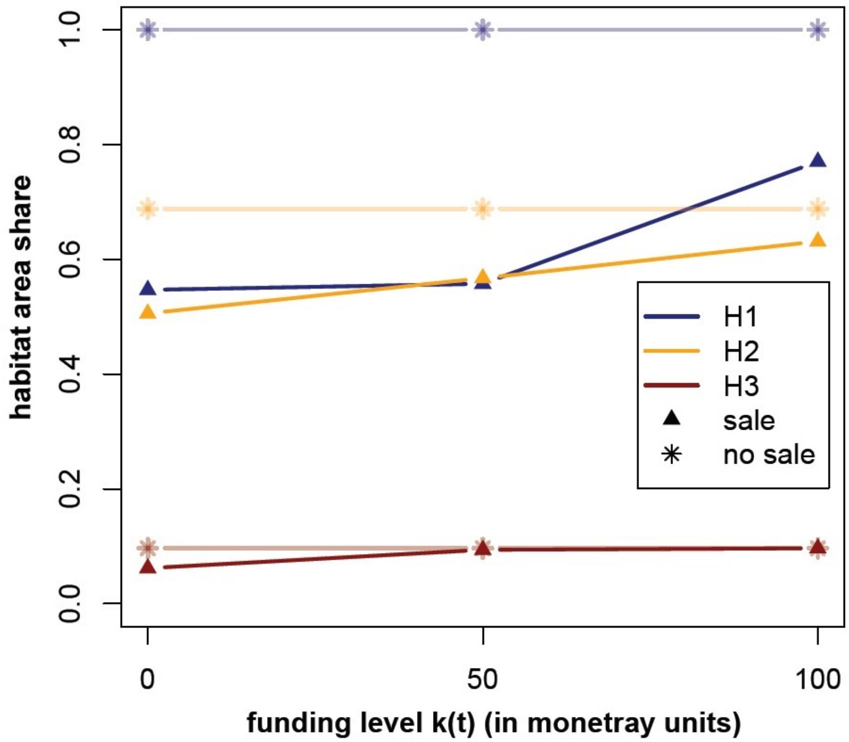


**Figure 6.** Habitat permanence measured as the % of the original habitat area maintained in all time steps depending on the level of funding.

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 sale tends to decrease habitat permanence when compared to the 'no-sale' case, but at the same time opens up the opportunity for habitat creation due to the increased flexibility of using available funds. However, the trade-off between permanence and flexibility looks different for the three habitat types: habitat type 3 suffers only marginally from area sale in terms of permanence, but improves drastically in terms of overall habitat area under 'sale'. Regarding habitat types 1 and 2, losses in permanence through 'sale' are more pronounced, while potential gains in habitat area over time under 'sale' are smaller.

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. We analyse two possible adaptation options: using additional funds for climate adaptation and selling sites that become increasingly less cost-effective. However, as selling reserve sites increases habitat turnover, a trade-off emerges between maximising habitat protection and maintaining permanence. We develop an optimisation approach to determine the optimal time series of reserve networks under climate change in a two-step procedure: we first solve the static optimisation problem to generate the optimal reserve network under current climatic conditions. We then solve a dynamic optimisation problem to adapt the reserve network over time. We adopt a *maximin* approach (Montoya et al., 2020) to solve the multi-objective optimisation using goal programming. We apply the model to analyse the trade-off between irreversible investments which have a limited adaptation potential and partially reversible investments which allow adaptations but may increase habitat turnover under climate change (i.e., whether selling of reserve sites is allowed). We examine the trade-off in a conceptual case study and specifically consider the impact of the size of additional funding for adaptation on the trade-off. Finally, we examine the cost of increasing habitat permanence under climate change. We would like to highlight three 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 extend. 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 and even under the assumption of perfect information (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 extend, 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 permanence of ’sale’ increases with the level of additional funding. When assuming that the main objective of the decision maker is to conserve all habitat types as well as possible, the changes in permanence with increasing funding may then serve as an indication of the marginal costs of increasing permanence. For example, we find that while for $H_1$ (the expanding habitat type), marginal costs decrease as the level of permanence is increased, marginal costs are relatively constant for $H_2$ (the shifting habitat type). For $H_3$ (the contracting habitat type), marginal costs increase as the maximum level of permanence is approached. Marginal costs of decreasing habitat turnover are hence particularly low for medium levels of permanence. For low levels of permanence, marginal costs are higher as the optimisation does not focus on the habitat type in question and hence requires higher habitat turnover to achieve the optimum. This result is hence driven by the optimisation, which optimises overall habitat areas rather than permanence. For high levels of permanence, marginal costs of increasing habitat permanence even further increase as reaching the maximum levels of permanence includes maintaining increasingly costly sites.

Third, 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) 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 extend, 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.

As in any model, we had to make some assumptions to simplify reality. First, we assume that the habitat is generated instantly, i.e. there is no time lag between the time that a grid cell is first conserved and the time when the grid cell contributes effective habitat area to the reserve network. 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., 2022). 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; Nath, 2020; 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 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 presented adaptation of the RD-problem is able to model the impact of different policy scenarios on conserving threatened habitat types under climate change. 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 avenues 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. If the conservation agency does not have perfect foresight (as it does in our model), the optimal investments in any time step may not be in line with the optimal investments given perfect information (Drechsler and Wätzold, 2020). In the case of imperfect foresight, the role of the quasi-option value of delaying irreversible investments (Arrow and Fisher, 1974) therefore provides an interesting avenue for future research on the optimal adaptation pathways of reserve networks under climate change (cp. Miller and Lad (1984), Albers (1996), Leroux et al. (2009), Brunette et al. (2014), Brunette et al. (2020)). 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 under climate change.

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# SUPPLEMENTARY MATERIAL

# A MODELLING THE LANDSCAPE

The elevation level $elev_i = 1 + \Big(sin\big((n(i)-5)(\pi/5)\big) + sin\big((m(i)-10)(\pi/10)\big)\Big)/2$ is assigned on a functional basis in a way that the landscape features three different regions, i.e. a valley, plains of medium elevation, and a mountain. In the elevation function, $n(i) \in [1,..,10]$ represents the column of the landscape in which cell $i$ is located, while $m(i) \in [1,..,20]$ represents the row (Fig. A.1).

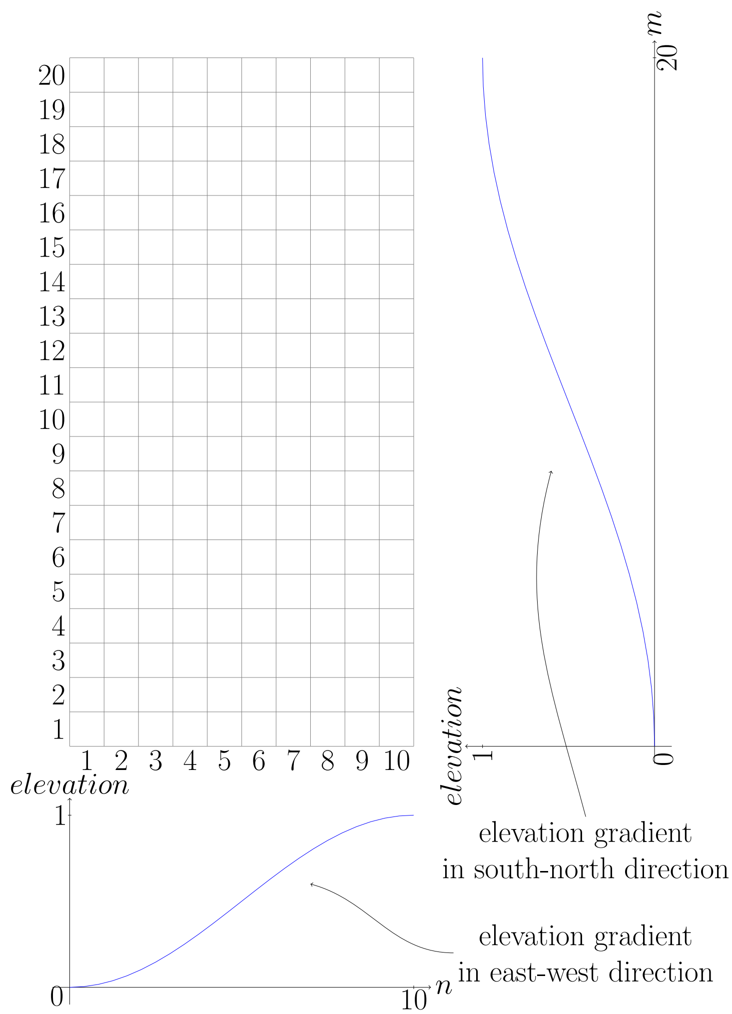


**Figure A.1.** Landscape grid in which conservation areas are selected (n=10 × m=20 cells), with the functional relationship describing the landscape's elevation in the east-west direction (below) and south-north direction (on the right).

# B UTILITY AND HABITAT TRANSITION FUNCTIONS

We measure the utility $h_{kit}$ of a grid cell for habitat type $H_k$ by considering a grid cell $i$'s suitability $S(H_{k,i}(t))$ at time $t$: the utility $h_{kit}$ of a grid cell for a chosen habitat type equals the percentage share of that habitat type's suitability on the summed suitabilities of all three habitat types, i.e. $h_{kit} = \frac{S(H_{k,i}(t))}{S(H_{1,i}(t))+S(H_{2,i}(t))+S(H_{3,i}(t))}$. We use a functional relationship of $S(H_{k,i}(t))$ to describe the individual climate-change-induced habitat shift of the three considered habitat types $k$ over time between $t = 1$ and $t = T$. The relationship depends on the elevation $elev_i$ of cell $i$. We model $S(H_{1,i}(t))$ as follows:

$$S(H_{1,i,t}) = \begin{cases} 0 & \text{if } elev_i < 0 \\ -B_1 + (1 + A_1 + B_1) elev_i * \frac{T - s_1 * t}{T} & \text{if } 0 \le elev_i < 1 \\ 1 & \text{if } 1 \le elev_i \end{cases} \tag{B.1}$$

$$S(H_{2,i,t}) = \begin{cases} 0 & \text{if } elev_i < 0 \\ 2 * elev_i * \frac{T - s_2 * t}{T} & \text{if } 0 \le elev_i < 0.5 \\ (2 - 2 * elev_i) * \frac{T - s_2 * t}{T} & \text{if } 0.5 \le elev_i < 1 \\ 0 & \text{if } 1 \le elev_i \end{cases} \tag{B.2}$$

$$S(H_{3,i,t}) = \begin{cases} 1 & \text{if } elev_i < 0 \\ 1 + B_3 - (1 + A_3 + B_3) elev_i * \frac{T - s_3 * t}{T} & \text{if } 0 \le elev_i < 1 \\ 0 & \text{if } 1 \le elev_i \end{cases} \tag{B.3}$$

See Figure B.1 for a graphical explanation of $A_k$ and $B_k$. $s_k$ represents a scaling factor regarding the strength of the influence of climate change and hence the speed of the northwards shift of $S(H_{k,i}(t))$ over time. For our study case we selected $A_1 = A_3 = B_1 = B_3 = 0$, $s_1 = s_3 = 1$, and $s_2 = 0.5$

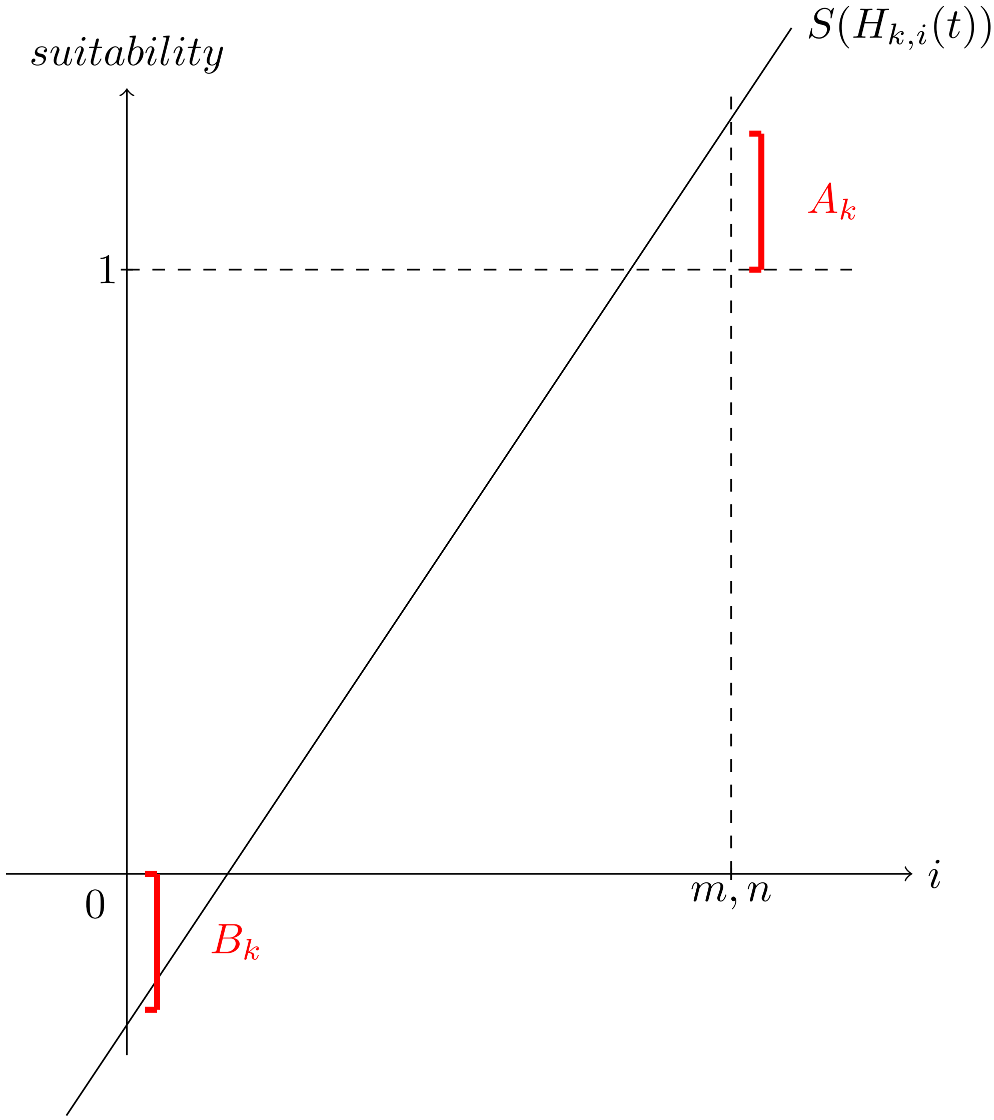


**Figure B.1.** Graphical illustration of parameters $A_k$ and $B_k$.

## C 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 C.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.

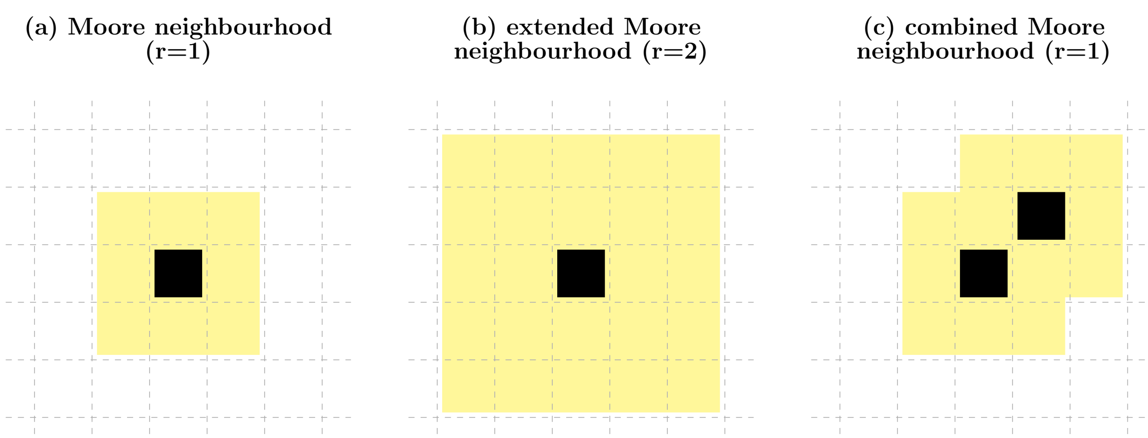


**Figure C.1.** Illustration of the (a) Moore neighbourhood ($d = 1$) of a grid cell, (b) the extended Moore neighbourhood ($d = 2$), and (c) the combined Moore neighbourhood of two cells ($d = 1$).