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Keep it or Leave it - the Role of Reversible Conservation Investments in Optimal Reserve Design under Climate Change

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Keep it or leave it - the role of reversible conservation investments in optimal reserve design under climate change

ABSTRACT

Climate change causes range shifts of species and habitats, thus making existing reserve networks less suitable in the future. In principle, reserve networks may be adapted to climate change in two ways: by providing additional funds and / or by allowing for the sale of sites to liquidate funds for new purchases. However, due to general negative ecological consequences, selling is often strongly regulated, thus rendering the optimal reserve design a problem of irreversible investment decisions. On the other hand, allowing for sale may be interpreted as an investment with costly reversibility, as involved transaction costs do not allow for full recovery of the initial investment. Whether allowing for the sale of sites to increase flexibility under climate change outweighs the costs of this increased flexibility remains an open question. We develop a conceptual climate-ecological-economic model to find the optimal solution for the reserve design problem under changing climatic conditions and different policy scenarios. These scenarios differ in terms of whether and when additional funds are provided, and whether selling of reserve sites is allowed. Our results show that the advantage of allowing for sales is large when no additional funds are available and decreases as the amount of additional capital provided for adaptation increases. Finally, providing a one-off payment initially instead of regular payments throughout the runtime of the model leads to higher habitat protection.

Keywords: Biodiversity conservation; conservation planning; climate adaptation; climate-ecological-economic modelling; ecological-economic modelling; habitat conservation; irreversible investment; investment of costly reversibility; RD-problem; 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 habitats caused by changing climatic conditions (Creutzburg et al., 2015; 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 with a given budget (Wätzold, 2014). To maintain cost-effectiveness and prevent the loss of certain habitat types, the reserve network may therefore have to be adapted under climate change. 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 the adaptations that have to be undertaken at every time step or the different options in terms of how to fund the adaptation.

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. However, these adaptation funding pathways may face several challenges: First, conservation funds are scarce and may not be large enough to expand the existing reserve network sufficiently. Second, 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 of existing reserve sites is often not permitted in practice (Fuller et al., 2010; Lennox et al., 2017), limiting the adaptation potential of reserves. However, in order to improve cost-effectiveness under climate change and prevent the loss of certain habitat types, the adaptation potential of the reserve may need to be increased (Gerling and Wätzold, 2021). One obvious option of increasing the adaptation potential

under climate change is the option of selling.

Climate change therefore adds a new dimension to the trade-off faced by a decision-maker of whether or not to allow for selling of reserve sites (Strange et al., 2006): 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-effectiveness. However, 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, albeit cautioning against general recommendations of allowing for selling (Alagador et al., 2014, 2016; Lennox et al., 2017). Given the limited amount of research on the value of allowing for sales under climate change, especially from an economic perspective, we aim to gain some conceptual understanding on whether and when allowing for sale may be warranted.

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 selling 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). Against this background, the question of whether or not to allow for the sale of reserve sites can therefore be interpreted as a trade-off between an irreversible investment problem (with limited flexibility for adaptation) and an investment under costly reversibility (with both positive and negative ecological consequences arising from the increased flexibility).

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, 2020b; 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, 2020b). 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, 2020a; 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 indicators 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, 2020) are therefore included more commonly.

(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 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). Recent work in this field adds the temporal dimension in multi-period RD-problems (Jafari et al., 2017) and considers different strategies of conservation planning in adapting existing reserve networks (van Langevelde

et al., 2002). However, with the notable exception of Alagador and Cerdeira (2020), considering the dynamic challenges of climate change has only rarely been attempted.

(4) **The RD-problem in the field of optimization at a conceptual level.** 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). 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 conceptual climate-ecological-economic model to investigate the trade-off between irreversible conservation investments and investments that are reversible at a cost under climate change. We consider a landscape of potential reserve sites. A conservation agency aims to create the optimal reserve network under climate change. 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. A conservation agency initially owns the optimal set of reserve sites given initial climatic conditions.

In our results, we start by illustrating how the ecological effectiveness of the initial reserve network changes under climate change if the reserve network is not adapted. We then consider the trade-off between irreversible investments and investments that are reversible at a cost under climate change and explicitly distinguish between cases of no, low and high levels of additional funding. Finally, we explore whether a larger flexibility in terms of when to spend the money provides any additional value. To do this, we examine whether there is any advantage in having an appropriately discounted sum of initial capital rather than the equivalent amount received at regular intervals.

2 MATERIALS AND METHODS

2.1 Model setup

We base our research on the MSCP and adapt it to fit the specific scope of our model. To ensure our results are not biased by initial conditions, we first solve a static optimisation problem by applying a *maximin* approach (Montoya et al., 2020) subject to a budget constraint. We then consider that over time, the quality of each habitat type within different areas of the reserve network will vary due to changing climatic conditions. We again apply a *maximin* approach subject to a budget constraint and the policy scenario in order to identify sites for purchasing and selling and create the optimal reserve network under dynamic conditions.

We utilize the JuMP modelling language (Dunning et al., 2017) in the Julia programming environment (Bezanson et al., 2017) to set up the climate-ecological-economic 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).

2.2 Modelling of the landscape, habitat types and climate change

The landscape in our model consists of a grid of $N = 10 * 20 = 200$ equally sized cells with 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. 1, and see Supplementary Material A and Fig. A.1 for details on the construction of the landscape).

In this landscape three different habitat types exist (H_1, H_2, H_3), each of which can be considered a potential home to multiple species. The utility h_{kit} of a grid cell for habitat type H_k depends on 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. $h_{kit} = \frac{S(H_{k,i}(t))}{S(H_{1,i}(t)) + S(H_{2,i}(t)) + S(H_{3,i}(t))}$. When a grid cell is conserved, the effective habitat area generated for the different habitat types is given by their respective utilities h_{kit} . We assume there is

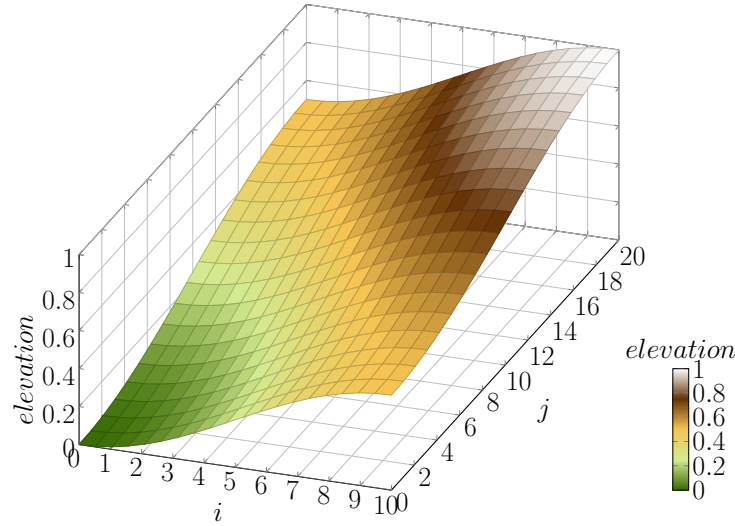


Figure 1. Landscape grid and grid cells, coloured by elevation level visualizing the topography of the landscape.

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.

The suitability $S(H_{k,i}(t))$ of a site for habitat type H_k depends on two factors: first, the elevation level $elev_i$ of grid cell i . 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 mountainous habitat type located in high elevations.

Second, the suitability $S(H_{k,i}(t))$ is time-dependent as the landscape faces changing climatic conditions over time. Climate change is 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. Rather than modelling climate change explicitly, e.g. through changes in precipitation or temperature on a grid cell level, we model it implicitly by assuming that the climatic changes cause the suitability for habitat type H_k of each grid cell i 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 2 illustrates the suitability of each habitat for all elevation levels for time steps $t = \{1, 5, 9, 13\}$ (see Supplementary Material B for details on the underlying functional relationship of $S(H_{k,i}(t))$).

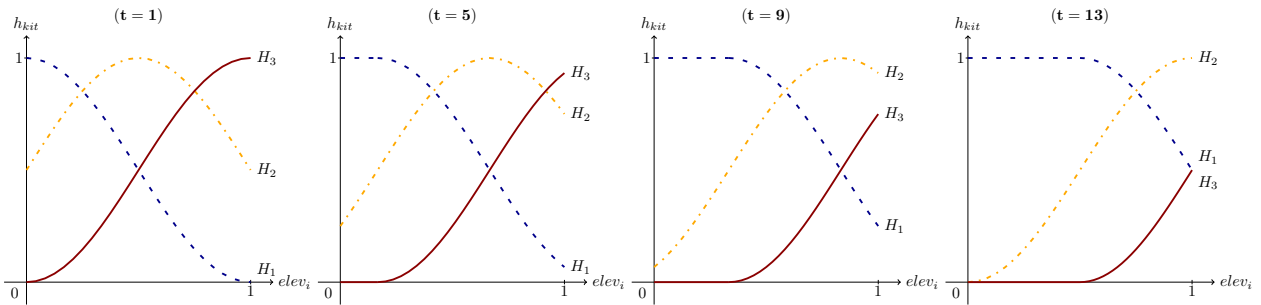


Figure 2. Utility level h_{kit} of a cell i at time steps $t \in \{1, 5, 9, 13\}$ for all three habitat types $k \in \{1, 2, 3\}$.

2.3 Decision problem of the conservation agency and policy scenarios

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 . This initial optimisation problem is formulated, and the solution procedure described, in section 2.4.1.

We then determine an adaptation strategy over a 60-year period, divided into twelve periods of five years each, that maximises conservation outcomes with respect to the three habitat types. As a result, a dynamic reserve network is generated – starting from the already existing initial reserve network and against the background of changing climatic conditions – by buying and selling chosen reserve sites. This dynamic optimisation problem is formulated and the solution procedure described in section 2.4.2.

Both the optimal initial selection of reserve sites and the strategy for selecting future reserve sites is subject to budget and proximity constraints on purchases and possible legal restrictions on selling defined in different policy scenarios (for details, see 2.4.1 and Supplementary Material C). We consider different policy scenarios in which the agency may or may not have an additional budget $k(t)$ available in every time step $t \in \{1, \dots, T\}$ to realise the reserve network adaptation. Depending on the policy scenario, this budget is comprised of different components, such as an upfront (one-off) budget paid in the beginning of $t = 1$, a regular budget paid in the beginning of each time step $t \in \{1, \dots, T\}$, any remaining budget from the previous period including interest payments, and funds from selling cells $((1 - a) * p_{ij})$ net of transactions costs a (measured as a fraction of the original price of that site p_{ij}). Buying and selling occurs throughout each five-year period but for simplicity we assume that all transactions occur halfway through the period and thus incur corresponding interest. 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.

Further details of the optimisation procedure of the initial and future reserve network, and the sense in which we mean "optimal" in the multi-objective optimisation follows in sections 2.4.1 and 2.4.2.

We then analyse the model and its outcomes in different policy scenarios. These scenarios differ

Policy scenario	Adaptation	Reversibility of investments	Additional funding	Question
static	no	no	no	1, 2
sale - no funding	yes	yes	no	2
sale - low funding	yes	yes	regular	3
sale - high funding	yes	yes	regular	3
no sale - low funding	yes	no	regular	3
no sale - high funding	yes	no	regular	3, 4
no sale - upfront funding	yes	no	upfront	4

Table 1. Overview of policy scenarios.

in whether selling is allowed or not and whether additional funding is provided. Table 1 provides an overview of these scenarios. Each policy scenario is then used to answer one or several of the following questions which are related to the individual scenario's conditions:

1. If no adaptation takes place, what happens to the habitat values of the initial reserve network as the climate changes?
2. In the absence of any new capital, can we improve the habitat values by selling some existing reserve sites and using the money to buy new sites?
3. Conservation agencies are often not allowed to sell a reserve site. Under climate change, and with some additional funding, would it be better to allow the sale of some sites to provide more capital to purchase new sites?
4. If a regular source of funds has been guaranteed, would it be better to convert this into its present value and have all the capital available immediately?

2.4 Optimisation procedure

To ensure that our analysis of management strategies under climate change is not tainted by the initial conditions, we first solve the standard reserve design problem. This involves the optimal selection of sites that meets habitat goals subject to constraints as described below. This optimal reserve network is then used as the starting point as we investigate the consequences of climate

change for the three habitat types under various policy scenarios.

2.4.1 Formulation of the initial optimisation problem

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 2 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.

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

$$\sum_{j \in M_{i+}} y_{ji} \leq 1 \quad \forall i \in N \quad (2)$$

$$y_{ij} \leq x_{ij} \quad \forall i \in M_{j+}, \forall j \in N \quad (3)$$

$$x_{ij} \leq B * y_{ij} \quad \forall i \in M_{j+}, \forall j \in N \quad (4)$$

$$\sum_{i \in N} y_{0i} = 1 \quad (5)$$

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

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 $y_{i,j} = 1$, 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 <i>source</i> node
N_+	set of all site nodes plus the <i>source</i> 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 <i>source</i> 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}	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 2. 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:

$$g_k = \max \sum_{j \in N} \sum_{i \in M_{j+}} y_{ij} * h_{kj} \quad k = 1, 2, 3. \quad (7)$$

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 ε

(cp. equation 8). Thus we replace the previous objectives and add a new constraint to the previous constraints, as given below.

$$\begin{aligned} \min \quad & \varepsilon \quad \text{subject to:} \\ & (g_k - \sum_{j \in N} \sum_{i \in M_{j+}} y_{ij} * h_{kij}) / g_k \leq \varepsilon \quad \text{for } k = 1, 2, 3 \end{aligned} \quad (8)$$

2.4.2 Formulation of the dynamic optimisation problem

We expect the habitat quality of the initially optimal solution to deteriorate with time under climate change. In this section we therefore formulate a dynamic optimisation model that allows for adaption of the initial reserve network through buying and selling of sites during each of twelve five-year periods.

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. Table 3 provides an overview of sets, indices, parameters and variables used in the mathematical formulation of the dynamic optimisation procedure.

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 is set at $c(0) = k(0)$. The dynamic system is subject to the following constraints.

$$\sum_{\{i,j\} \in N} (1 + a) * p_{ij} * b_{ijt} \leq c(t) \quad \forall t \quad (9)$$

$$c(t+1) = (1+r)^5 * c(t) + k(t) + (1+r)^{2.5} * \sum_{\{i,j\} \in N} (1-a) * p_{ij} * s_{ijt} - (1+a) * p_{ij} * b_{ijt} \quad \forall t \quad (10)$$

$$y_{ijt+1} = y_{ijt} + b_{ijt} - s_{ijt} \quad \forall \{i,j\} \in N, \forall t \quad (11)$$

$$b_{ijt} \leq \sum_{\{kl\} \in M_{ij}} (y_{klt} - s_{klt}) \quad \forall t \quad (12)$$

$$b_{ijt} \leq 1 - y_{ijt} \quad \forall \{i,j\} \in N, \forall t \quad (13)$$

$$\mathbf{M}(1 - s_{ijt}) \geq \sum_{\{kl\} \in M_{ij}} y_{klt} - 1 \quad \forall t \quad (14)$$

Symbol	Description
site $\{i, j\}$	indicates the site located at row i and column j in the $n \times m$ grid
N	set of all sites $\{i, j\}$
M_{ij}	set of all sites in the Moore neighbourhood of $\{i, j\}$
p_{ij}	price of site $\{i, j\}$
$h_{k,i,j,t}$	utility of type k habitat at site $\{i, j\}$ at time t
a	transaction cost of buying or selling a site
r	annual interest (discount) rate
$k(t)$	additional capital (e.g. from grants or donations) available from time t
y_{ijt}	1 if site $\{i, j\}$ is owned at time t , 0 otherwise
b_{ijt}	1 if site $\{i, j\}$ is purchased during the period $(t, t+1)$, 0 otherwise
s_{ijt}	1 if site $\{i, j\}$ is sold during the period $(t, t+1)$, 0 otherwise
\mathbf{M}	a large number

Table 3. Overview of used sets, indices, variables and parameters in the dynamic optimisation.

Constraint 9 ensures that the cost of purchases in any time period cannot exceed the capital available at that time. Constraint 10 keeps track of the flow of capital. Capital carried over from the previous period earns interest for the new five-year period. We assume that buying and selling transactions occur in the middle of the five-year term i.e. 2.5 years before the next period, thus sales and purchases must be adjusted according to the interest rate. 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 $\{i,j\}$ is not to be sold. Note that there are at most eight sites in the direct neighbourhood of any particular site. Thus setting $M=8$ is sufficiently large to ensure that the constraint will always be satisfied at any time that site $\{i,j\}$ is not sold. Constraints 12 and 14 together encourage rather than guarantee contiguity.

Objectives and solution procedure

While maximising habitat is desirable, our primary concern is loss of habitat. We therefore aim to maximise the minimum values of each habitat type. As we consider three habitat types we again have a multi-objective problem which we formulate using a goal programming approach. We begin by solving the following three problems subject to the constraints 9-14 given above.

For $k = 1, 2, 3$ solve:

$$\Gamma_k = \max \theta \quad (15)$$

$$\text{subject to: } \sum_{\{i,j\} \in N} h_{kijt} * y_{ijt} \geq \theta \quad \forall t \quad (16)$$

Having obtained the goals, Γ_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 constraints together with the objective as given below.

$$\begin{aligned} & \min \quad \varepsilon \\ & \text{subject to: } (\Gamma_k - \sum_{\{i,j\} \in N} h_{kijt} * y_{ijt}) / \Gamma_k \leq \varepsilon \quad \forall t, \quad k = 1, 2, 3 \end{aligned} \quad (17)$$

3 RESULTS

We first solve the static problem described in section 2.4.1 to generate a reserve network that is optimal under initial climatic conditions. Given an initial budget of 500μ (throughout this section we use μ to indicate monetary units), representing approximately 7% of the total value of all sites in the landscape, we follow the procedure described in section 2.4.2. This generates the reserve network shown in Figure 3(a), which is optimal for conditions at the initial time $t = 1$. Figure 3(c) shows the spatial distribution of the three habitat types in the landscape. It can be seen that the most prominent locations of H_1 are located in the bottom left corner of the reserve network (i.e. the valley part of the landscape), the largest areas of H_2 can be found more in the center of the landscape (i.e. the plains), while H_3 is found mainly in the upper right corner of the reserve network (i.e. the mountain).

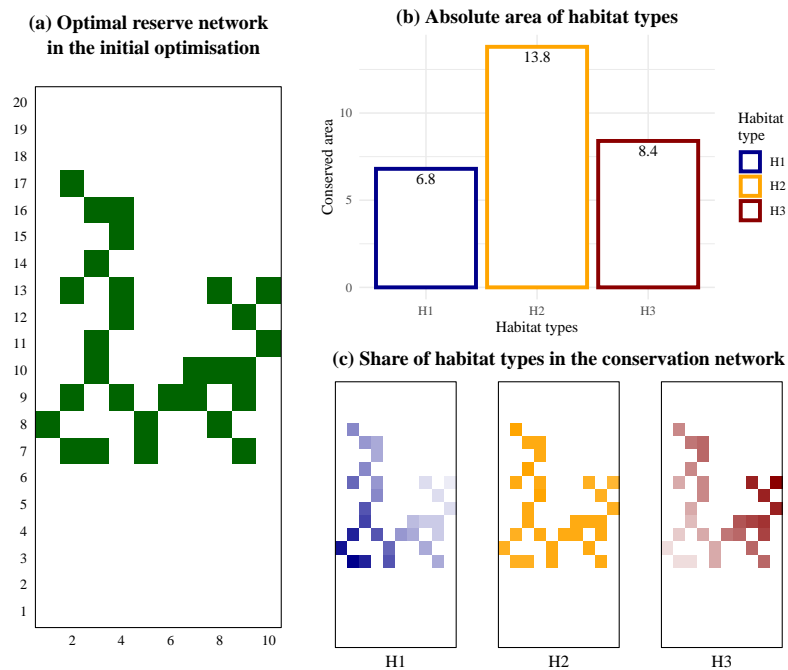


Figure 3. (a) Optimal reserve network within the landscape resulting from the initial optimisation. (b) Absolute area of the three habitat types within the initial optimal reserve network. (c) Share of each habitat type within the initial optimal reserve network. Lighter shaded areas represent a smaller share of the specific habitat type of a site, darker shaded areas represent larger shares.

The total habitat value of each habitat type in the initial optimal reserve network is shown in

Figure 3(b). In order to represent all three habitat types optimally, the initial reserve network turns out to be located in the center of the landscape, as was to be expected. Due to the initial utilities of the cells with respect to the habitat types (cp. Fig. 2), habitat H_2 covers the largest area which represents approx. 15% of the potentially available habitat area for this habitat type in the whole landscape. This is unsurprising as in the initial reserve, the center of the landscape provides ideal conditions for that specific habitat type. The other habitat types on the other hand find better respective conditions in the valley (lower left section of the landscape, for H_1) or the mountain (upper right section, for H_3). Hence, the respective area covered is smaller, while the share of the overall available potential habitat area in the landscape is of similar magnitude (approx. 14% each).

We now proceed to address questions 1 and 2:

1. *If no adaptation takes place, what happens to the habitat values of the initial reserve network as the climate changes?*
2. *In the absence of any new capital, can we improve the habitat values by selling some existing reserve sites and using the money to buy new sites?*

In either case, no additional capital is provided to the agency, i.e. all new sites are bought with capital acquired from the sale of other sites. It is clear from Figure 4(a) that in the absence of any reserve network adaptation, habitat type H_3 is almost lost. Some of this is unavoidable as the total potential area of habitat type H_3 in the whole landscape has declined to about 15% of its original value. Nevertheless, at the final time step $t = 13$, the total habitat value of H_3 in the reserve network is less than 10% of the available potential habitat area in the landscape, whereas the strategy involving selling and buying (Fig. 4(b)) achieves a total habitat value of H_3 that exceeds 52% of that available area. The other two habitat types also do better under the sell strategy.

We now address question 3:

3. *Conservation agencies are often not allowed to sell a reserve site. Under climate change, and with some additional funding, would it be better to allow the sale of some sites to provide more capital to purchase new sites?*

When the agency receives additional funding, the reserve network may be adapted to some extent

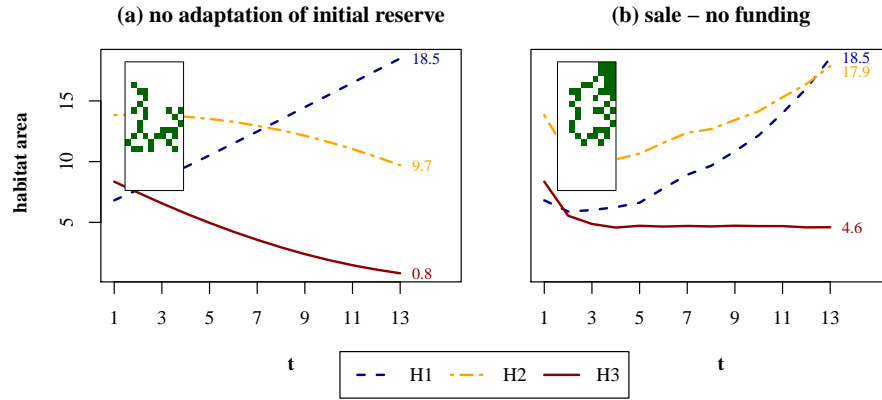


Figure 4. Development of habitat values for the 'static' policy scenario (a) and the 'sale - no funding' policy scenario (b). The number to the right of the lines shows the habitat value for each habitat type in the last time step.

even without the option of selling. Here, we compare the 'no sale' policy with the 'sale' policy under two budget constraints, which, for convenience, we shall call the 'low funding' and the 'high funding' cases. In the 'low funding' case we will assume that the agency receives 50μ 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 100μ .

Habitat type H_3 is the most negatively affected by climate change. Effectively this means that the optimisation problem is directed at maximising the minimum habitat values of type 3. In the 'low funding' case, the minimum value of habitat type H_3 improves by more than 10% when sales are allowed compared with the 'no sale' case (Fig. 5(a) and (b)). Hence, the 'sale' option is preferable over the 'no sale' option in the 'low funding' case. Regarding the 'high funding' case, the outcome for habitat type H_3 is no better under the 'sale' than the 'no sale' strategy in the final time step (Fig. 5(c) and (d)). Hence, both options are similar in their final outcome for H_3 and the advantage of the 'sale' option ceases in the high funding case.

Finally, we address question 4:

4. *If a regular source of funds has been guaranteed, would it be better to convert this into its present value and have all the capital available immediately?*

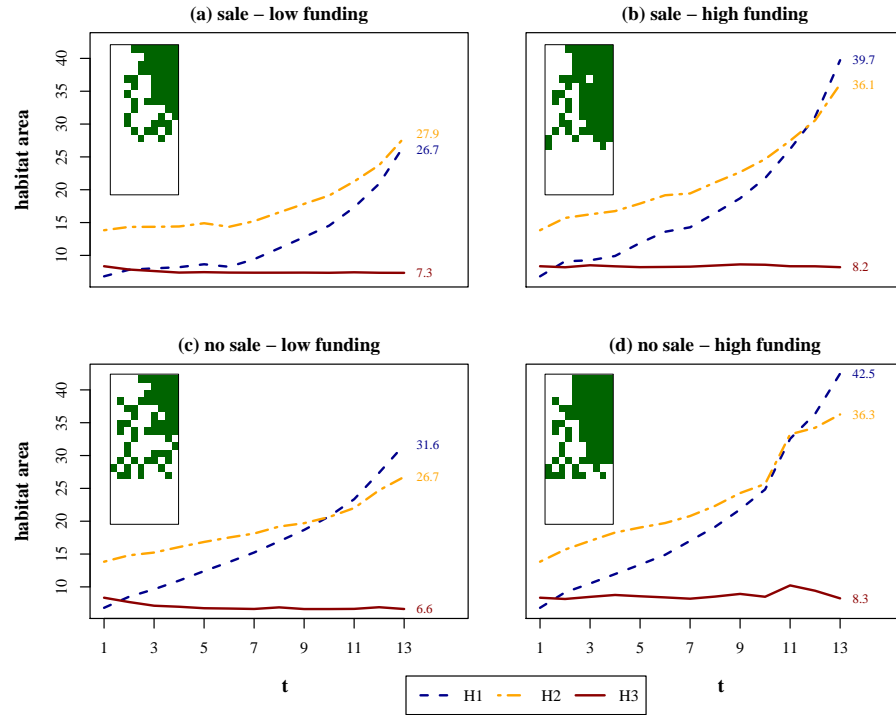


Figure 5. Development of the habitat values for the 'sale - low funding' (a), 'no sale - low funding' (c), 'sale - high funding' (b) and 'no sale - high funding' (d) policy scenarios. The number to the right of the lines shows the habitat value for each habitat type in the last time step.

We consider the case of the agency receiving a regular payment of 100μ at the start of each of the twelve five-year periods. At the 5% interest rate level used throughout this work, this is equivalent to a present value of 437.22μ at the initial time, $t = 1$. We selected a level of 5% interest rates as interest rates in general did not influence the results very strongly. As there are only negligible differences between solutions with and without sales for the 'high funding' scenarios, we conduct the comparison only with the 'no sale' model.

The results shown in figure 6 indicate that better outcomes can be achieved with a single upfront payment than with the equivalent capital in regular payments. The habitat value for H_1 , i.e. the 'valley habitat', is initially the most threatened habitat type. With an upfront payment, its initial value improves slightly compared to regular payments. In the final time step, habitat type H_3 (the 'mountain habitat') is the most endangered. The upfront payment leads to a (slightly) larger protection of this habitat type in the final time step compared to the regular payments case. Similarly,

the final outcome for habitat type H_2 also improves (slightly) in the upfront payment case. This suggests that the increased flexibility in terms of when to spend the money renders upfront payments superior to regular payments.

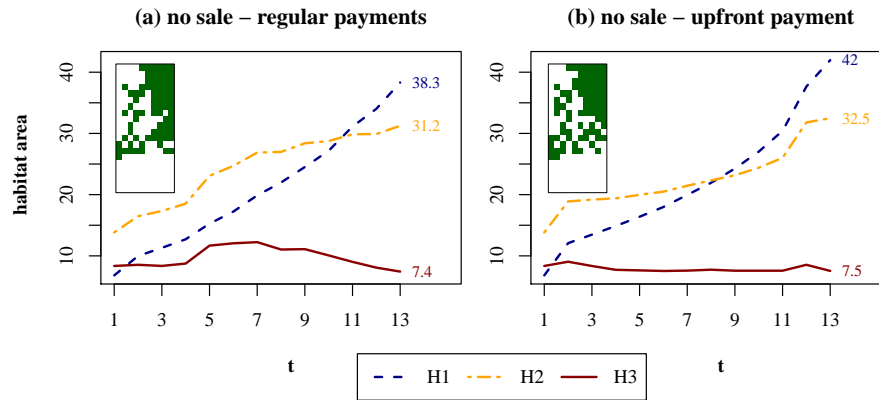


Figure 6. Development of the habitat values for the regular payments (a) and upfront payment (b) policy scenarios. The number to the right of the lines shows the habitat value for each habitat type in the last time step.

4 DISCUSSION AND CONCLUSION

We present a specific case of the reserve design problem (RD-problem) in which the suitability of potential reserve sites changes over time due to climate change. We adapt the Maximal Species Covering Problem (MSCP) to maximise the conservation outcome given a budget constraint in a two-step optimisation 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. Our optimisation procedure considers specifically the adaptations that have to be undertaken at every time step. We apply the model to analyse the trade-off between irreversible and partially reversible investments under climate change (i.e., whether selling of reserve sites is allowed), and specifically consider whether and when additional funding is provided. We would like to highlight three key results.

First, and in line with ecological research (see for example Heller and Zavaleta (2009); Vincent

et al. (2019)), our results show that a static reserve network optimised for initial climatic conditions becomes increasingly less valuable for some habitat types, while the expanding habitat type benefits from this approach. Thus, the habitat type that becomes the most threatened under climate change is the least well protected in this static approach. This case implicitly assumes that the conservation agency is unable to adapt the existing reserve network due to budget and legal restrictions or is unaware of the need to do so. While in reality, many conservation actors are aware of the need to consider climate change in conservation decision-making, this is often not done due to a lack of information necessary for "climate-smart" decision-making (Hannah et al., 2002; Prober et al., 2017). Our results therefore provide further evidence for the call of ecologists that reserve networks need to be expanded to maintain the protection of habitat under climate change (Heller and Zavaleta, 2009; Vincent et al., 2019). Additionally, with this scenario we aim to increase awareness of the importance of including climate change impacts as a variable in optimal reserve design problems. So far, this is only rarely included.

Second, 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') 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; Lennox et al., 2017). The possibility of selling provides value as the conservation agency does not have to commit initially to irreversible investments (Ando and Hannah, 2011). 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). Our research suggests that another important factor influencing this trade-off is whether, and to what extent, other sources of funding are available for adapting the reserve network.

Third, we investigate in how far the flexibility of receiving additional funds as a one-off payment rather than regular payments throughout the runtime of the model influence the optimal outcome. Our results show that indeed the increased flexibility in terms of when to spend the money improves the overall outcome that can be achieved. This is in line with previous research on the topic (Costello and Polasky, 2004). However, 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. Brunette et al. (2014) and Brunette et al. (2020)).

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, 2020; 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 new (former) sites, the cost-effectiveness is further reduced 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. The model was able to show that reserve networks need to be adapted under changing climatic conditions in order to remain suitable under climate change. In particular, the model can be used to analyse different policy scenarios such as whether or not to allow for sale, i.e. whether or not investments are irreversible. With this model, we aimed to gain some conceptual understanding on the trade-off between irreversible and partially reversible conservation investments under climate change. It was shown that this trade-off is influenced by whether (and to what extent) additional funds for adaptation are available. In future research, the model may serve as a tool to study the complexities of specific case studies in greater detail. For example, given the implementation of the optimisation, the model may easily be expanded to consider the parametrisation of specific case studies, landscapes that do not consist of grid cells but vectors of any shape and size (Jafari and Hearne, 2013), time lags or "conservation credit" (Watts et al., 2020), and changing opportunity costs if the necessary information for the case study-specific parametrisation is available. 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 in this field may provide important insights in how to conserve biodiversity cost-effectively under climate change.

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SUPPLEMENTARY MATERIAL

A MODELLING THE LANDSCAPE

The elevation level $elev_i = 1 + \left(\sin((n(i) - 5)(\pi/5)) + \sin((m(i) - 10)(\pi/10)) \right) / 2$ 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, $n(i) \in [1, \dots, 10]$ represents the column of the landscape in which cell i is located, while $m(i) \in [1, \dots, 20]$ represents the row (Fig. A.1).

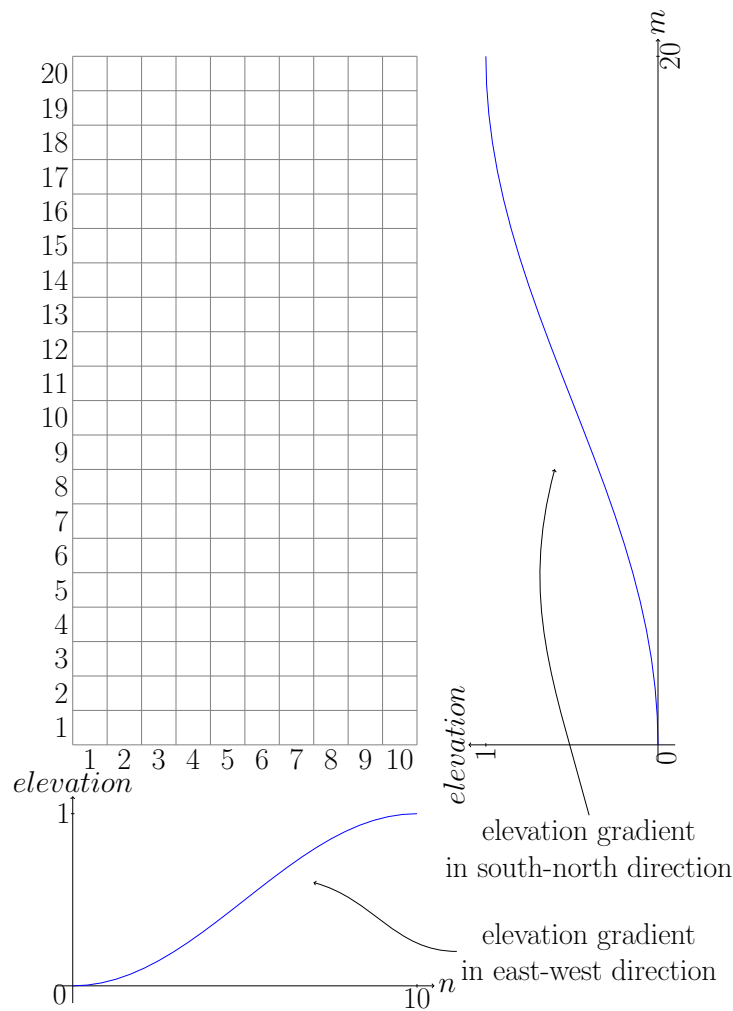


Figure A.1. Landscape grid in which conservation areas are selected ($n=10 \times m=20$ cells), with the functional relationship describing the landscape's elevation in the east-west direction (below) and south-north direction (on the right).

B HABITAT TRANSITION FUNCTIONS

We used 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 modeled $S(H_{1,i}(t))$ as follows:

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

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

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

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 $s_2 = 0.5$

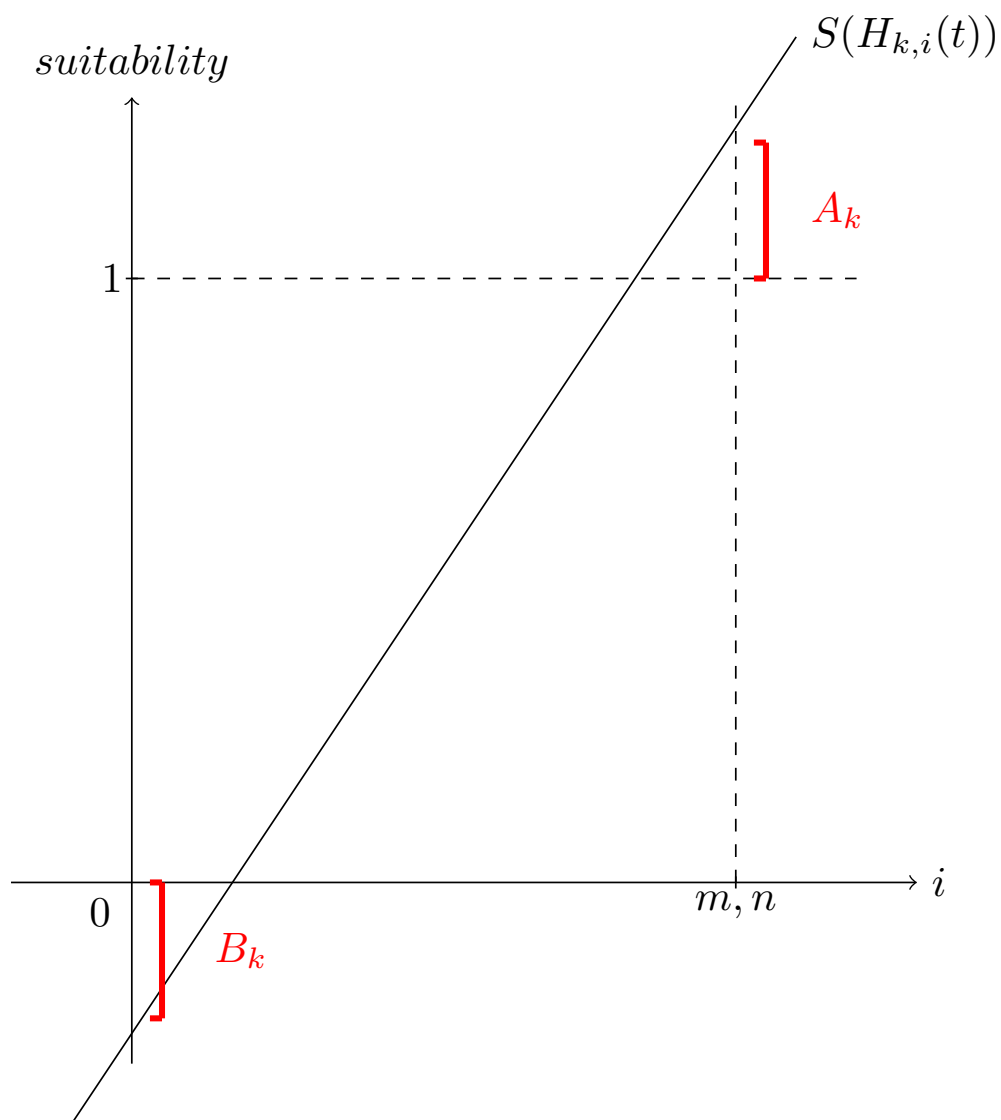


Figure B.1. Graphical illustration of parameters A_k and B_k .

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, 2020; 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.

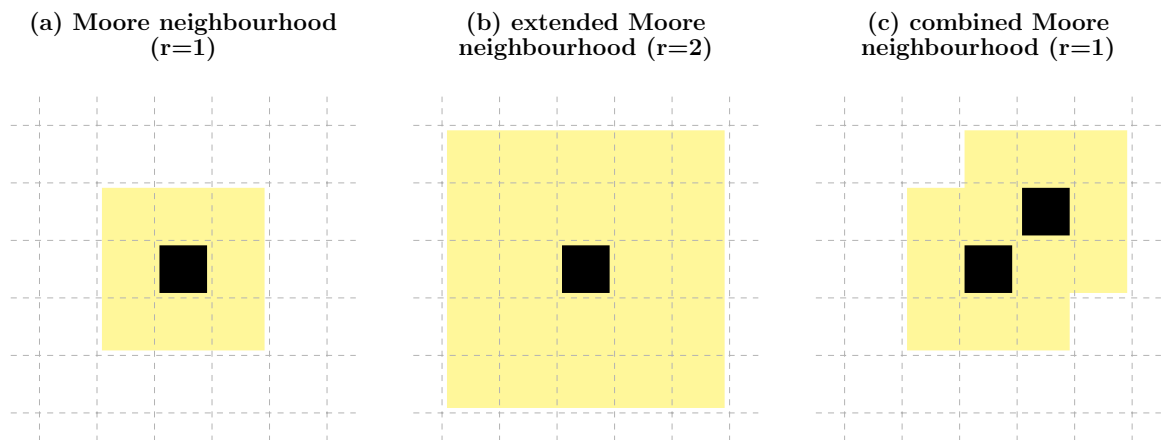


Figure C.1. Illustration of the (a) Moore neighbourhood ($d = 1$) of a grid cell, (b) the extended Moore neighbourhood ($d = 2$), and (c) the combined Moore neighbourhood of two cells ($d = 1$).