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Climate Change and the Cost-Effective Governance Mode for Biodiversity Conservation

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Abstract

Climate change poses a key challenge for biodiversity conservation. Conservation agencies, in particular, have to decide where to carry out conservation measures in a landscape to enable species to move with climate change. Moreover, they can choose two main governance modes: (1) buy land to implement conservation measures themselves on that land, or (2) compensate landowners for voluntarily carrying out conservation measures on their land. We develop a dynamic, conceptual ecological-economic model to investigate the influence of changes in climatic parameters on the cost-effectiveness of these governance modes and specific patch selection strategies (price prioritisation, species abundance prioritisation, climate suitability prioritisation, climate change direction prioritisation). We identify five effects that explain the cost-effectiveness performance of the combinations of governance mode and patch selection strategy and find that their cost-effectiveness depends on climate parameters and is thus case-specific.

Keywords Agri-environment scheme · Biodiversity · Climate-ecological-economic modelling · Conservation payments · Cost-effectiveness · Land acquisition · Make-or-buy decision · Payments for environmental services · Modes of governance

1 Introduction

Financial resources for biodiversity conservation projects are scarce. A cost-effective use of these resources—understood as maximising conservation goals for given financial resources or minimising financial resources to achieve given goals—is thus of the utmost importance (Ando et al. 1998; Ferraro and Pattanayak 2006). A growing field of research hence focuses on the cost-effectiveness analysis of biodiversity conservation policies (Ansell et al. 2016; Drechsler 2017; Wätzold et al. 2016). Examples include studies on the cost-effective selection of habitat types (Petersen et al. 2016), conservation in an

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uncertain environment (Armsworth 2018), the cost-effective design of conservation payments (Drechsler et al. 2016, 2017), the empirical assessment of conservation contracts (Hily et al. 2015; Schöttker and Santos 2019), and the spatial differentiation of conservation payments (Armsworth et al. 2012; Lewis et al. 2011; Wätzold and Drechsler 2014).

A novel perspective regarding the cost-effective design of conservation measures is related to the application of Williamson's analysis of the firm and the related "make-or-buy" decision (Williamson 1998, 1989) to biodiversity conservation (Schöttker et al. 2016; Wang et al. 2016). In this context it is of interest how the conservation agency chooses among several alternative governance modes representing different levels of vertical integration of conservation measure provision into the agency's organizational structure. Following Schöttker et al. (2016), we assume that, in principle, conservation agencies have the choice of two governance modes: (1) to buy land and implement biodiversity conservation measures on this land themselves or through a contractor, e.g. a farmer (*buy alternative*), or (2) to compensate landowners for voluntarily implementing conservation measures on their own land by offsetting implementation costs with a compensation payment (*compensation alternative*).

Examples for both governance modes can be found around the world. Considering the *buy alternative*, an illustrative example is the nature conservation foundation "Stiftung Naturschutz Schleswig Holstein", which owns approximately 2.4% of the total land area of the federal state of Schleswig Holstein (www.stiftungsland.de) in Germany, substantial parts of which are extensively managed by farmers to generate specific conservation outcomes (Schöttker and Wätzold 2018). In the UK, the Royal Society for the Protection of Birds owns and (partly actively manages) more than 1150 km² of land (www.rspb.org.uk), and in the US, The Nature Conservancy owns and manages 8000 km² of land (www.nature.org; Pinnschmidt et al. 2021). For other examples of conservation agencies purchasing and actively managing land see Mattijssen et al. (2018) for The Netherlands, Zoomers (2011) for Argentina, and Xie et al. (2020) for case studies across the globe. Regarding the *compensation alternative*, an example is the "Natur plus Standard" in Germany. Here, landowners who voluntarily implement conservation measures receive a certificate that can be sold to private actors, creating a contract relationship, which secures the provision of biodiversity enhancement (www.naturplus-standard.de). Other examples of privately financed compensation payments can be found in the US (Ferraro and Simpson 2002; Sorice et al. 2013), Cambodia (Clements et al. 2010) and Costa Rica (Redondo-Brenes and Welsh 2010) among others.

There is a small but increasing body of literature that analyses the question of governance mode in the context of biodiversity conservation. This literature addresses aspects such as the conceptual analysis of optimal governance mode choice (Muradian and Rival 2012), the development of ecological-economic models to assess the cost-effectiveness of different governance modes (Schöttker et al. 2016), specific conservation settings like forestry and corresponding governance mode options in developed (Juutinen et al. 2008) and developing countries (Curran et al. 2016), and cost assessments of specific governance modes related to conservation projects (Schöttker and Santos 2019; Schöttker and Wätzold 2018). These studies suggest a substantial impact of governance mode choice on the cost-effective implementation of conservation policies.

A key threat to global biodiversity, which has not been discussed in the context of cost-effective governance modes, is climate change. According to Thomas et al. (2004) between 15 and 37% of species face a high risk of extinction due to climate change in sampled regions worldwide. Araújo et al. (2011) state that by 2080, 58% of currently protected species in Europe will lose their habitat due to climate-driven range shifts. In order

to conserve biodiversity in a changing climate, the development of climate change compatible conservation strategies and policies is important (Heller and Zavaleta, 2009; Jones et al. 2016; Reside et al. 2018). Suggestions generally stress the need to make conservation policies more adaptive (Cinner et al. 2018) and focus on the design of conservation policies that enable species to migrate towards the species' new ranges (Heller and Zavaleta 2009). However, most research in this field comes from ecologists and conservation biologists and focuses on the impact of conservation policies on species survival in a changing climate (e.g. Zomer et al. 2015; Ribeiro et al. 2018; Jacobs et al. 2019; Ainsworth and Drake 2020).

From an economic perspective, only a few studies analyse biodiversity conservation policies and strategies in a changing climate (Ando and Langpap 2018). Examples include the application of modern portfolio analysis for conservation site selection under climate change uncertainty (Mallory and Ando 2014), the investigation of the cost-effectiveness performance of different types of conservation payments (Hily et al. 2017) and the development of an economic evaluation framework for land-use-based conservation policy instruments in a changing climate (Gerling and Wätzold 2021).

The purpose of our work is to combine the two novel areas of the economic analysis of governance modes for biodiversity conservation and the economic analysis of biodiversity conservation under climate change. Specifically, we analyse the effects of governance mode choices on the cost-effectiveness of biodiversity conservation against the background of variations in climatic conditions. Our background is species conservation in cultural landscapes such as large parts of Europe in which (1) conservation depends on the availability of land and (2) where species are present due to a specific, often traditional, type of land use (Küster 2004). This implies that a conservation agency has to not only provide land with appropriate climate characteristics for a species but also ensure that specific conservation measures, often mimicking this traditional type of land use, are carried out on that land (for example specific mowing or grazing regimes for endangered grassland birds, Wätzold et al. 2016).

We develop a conceptual, spatially explicit ecological-economic model in a dynamic landscape, and estimate the cost-effectiveness of four different patch selection strategies for the two governance modes considered under climate change. These strategies include price prioritisation, species abundance prioritisation, climate suitability prioritisation and climate change direction prioritisation.

Our analysis focuses on the impact of climate parameters (climate change speed and different spatial climate characteristics) on the cost-effectiveness of different governance mode and patch selection strategy options. For this purpose, we analyse how changes in these climate parameters impact the cost-effectiveness of different governance mode and patch selection strategy options in a sensitivity analysis. As Schöttker et al. (2016) has already investigated the impact of ecological and economic parameters on the cost-effectiveness of different governance mode options in detail, we only briefly present results related to changes in ecological and economic parameters in Appendix D.

2 The Model

2.1 Model Overview

Our ecological-economic model consists of different components. Figure 1 presents a graphical overview of the model and visualizes the main dependencies of the components.

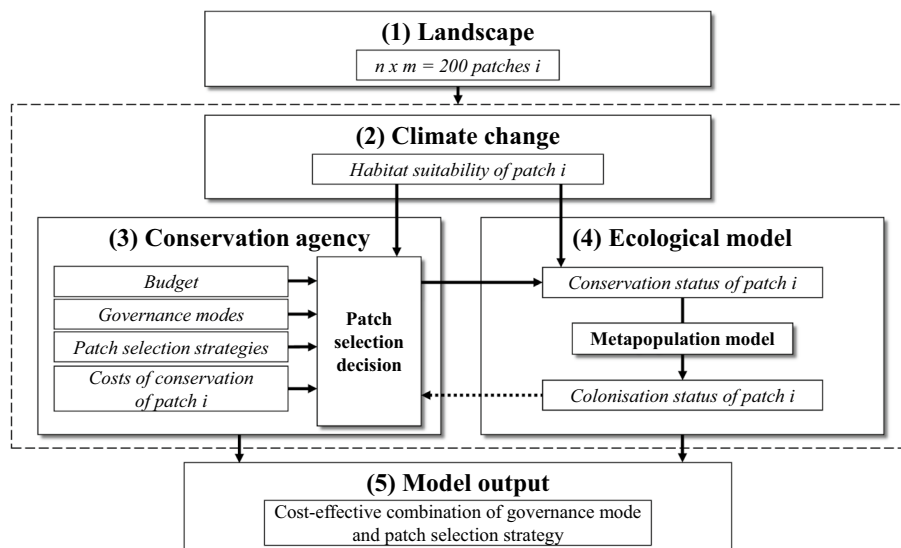


Fig. 1 Conceptual visualisation of the ecological-economic model. The boxes (1–5) represent key components of the model. The arrows highlight key connections between the different components

In our model, a landscape (Fig. 1, box 1) consists of patches which can be managed either for purely economic purposes or to provide habitat for an endangered species which colonises a subset of all habitat patches. The landscape faces changing climatic conditions over time (Fig. 1, box 2). We consider a conservation agency (Fig. 1, box 3) with a conservation budget to select patches in the landscape as habitat for the endangered species. For this purpose, the agency considers different governance modes and develops different patch selection strategies, which take into account (patch specific) conservation costs, climatic conditions and habitat colonisation status.

For the different combinations of governance modes and patch selection strategies, the decision process of the agency results in different sets of patches selected as habitats for a given budget. This information feeds into the ecological model (Fig. 1, box 4) together with the patch specific climatic conditions. Based on metapopulation dynamics, i.e. the colonisation, extinction and migration processes of the target species in the landscape, and the available habitats, the ecological model determines the conservation success. The described procedure is simulated over 100 time steps to take into account climate change and to reflect species' migration processes. In each time step, a new patch selection decision is made by the conservation agency, which is influenced by the ecological processes from the previous time step (dotted arrow between box 3 and 4), and – together with (continuously) changing climatic conditions – triggers again a new evaluation from the ecological model.

Finally, the model evaluates the conservation successes of the different combinations of governance modes and patch selection strategies for a given budget. The conservation success is measured in terms of share of simulation runs in which the target species goes extinct in the complete landscape within 100 time steps, i.e. the landscape level extinction rate. This evaluation enables us to compare the different combinations of governance modes and patch selection strategies in terms of their cost-effectiveness (Fig. 1, box 5).

2.2 Landscape and Conservation Costs

We assume a landscape with $10 \times 20 = 200$ equally sized, square patches i (Table 1 provides an overview of all variables used in the model and Table 2 of all parameter values used in the computation). The landscape has a size of 10 patches in the east–west dimension and 20 patches in the south–north dimension (Fig. 2a). Assuming a rectangular rather than quadratic landscape facilitates the modelling of changing climatic conditions. A length of 20 patches in south–north direction allows for a substantial variation of climate suitability for species conservation throughout the whole landscape and at patch level over the whole timeframe of the simulation (Sect. 2.3 provides details on how climate change is modelled).

Table 1 Overview and description of model variables

Variable name	Variable description
B^{buy}	Total budget for purchasing patches
B_t^{buy}	Budget to purchase land within a specific time step t
B^{comp}	Total budget to compensate landowners
B_t^{comp}	Budget to compensate landowners within a specific time step t
$c_i^{cons}(t)$	Conservation status of patch i
$c^{comp}(t)$	Necessary compensation payment for each patch under conservation in the compensation alternative in time step t
c_i^{buy}	Total expenses to buy a patch i
c_i^{sell}	Total amount of money received when selling a patch i
$cs_i(t)$	Climate suitability of patch i at time step t
d_{ij}	Distance between patches i and j
$e_i(t)$	Local extinction probability of patch i in time step t
ϵ	Residual budget in the compensation alternative
$h_{i,t}$	Dummy variable to indicate if a patch i is colonised at time step t
$Im_{i,t}$	Immigration rate into patch i at time step t
K	All patches within the climatically suitable zone
mc_i	Monitoring costs of patch i
μ_t	Centre of the climate suitability bell curve at time step t
$oc(t)$	Maximum opportunity costs of conservation of all patches participating in the compensation alternative at time step t
p_i^{buy}	Purchasing price of a patch i
$\overline{p^{buy}}$	Mean purchasing price of patches in the landscape
S	Number of all climatically suitable patches that can be reached by dispersal of the target species from already occupied patches
$\sigma_{p^{buy}}$	Standard deviation of purchasing prices
t	Time step
$\tau_{i,t}$	Colonisation probability of patch i at time step t
tc_i^{buy}	Transaction costs of purchasing a patch i
$tc^{comp}(t)$	Maximum transaction costs to compensate the landowner with the highest opportunity costs in the compensation alternative
(x_i, y_i)	Coordinates of patch i

Table 2 Overview and description of parameters and parametrisation values specified for computation of the Monte Carlo Simulation and the sensitivity analysis

Parameter	Parameter description	Parametrisation value
i	Patch index	$\in [1, 200]$
Economic parameters		
\overline{OC}	Mean opportunity costs in the landscape*	1.0
σ_{OC}	Standard deviation of opportunity costs \overline{OC}	0.1
\overline{IC}^{buy}	Mean transaction costs of purchasing a patch*	0.1
σ_{IC}	Standard deviation of transaction costs	0.01
\overline{MC}	Mean monitoring costs*	0.1
σ_{MC}	Standard deviation of monitoring costs	0.01
B^{buy}, B^{comp}	Total budget available in the two governance modes*	1000
r	Interest rate*	0.03
Ecological parameters		
v	Emigration rate from any patch*	100
θ	Immigration threshold for successful colonisation	5
δ	Dispersal distance of the target species*	1
Climate parameters		
T	Maximum number of time steps	Value range $\in \{50, 100, 150\}$
c_{cl}^{thr}	Climate suitability threshold	Base case 100
ρ	Curvature of the climate suitability bell shape	$\in \{0.3, 0.5, 0.7\}$
λ	Scaling factor for patch selection strategy 'climate suitability prioritisation'	$\in \{2, 3, 4\}$
κ	Scaling factor for patch selection strategy 'climate change direction prioritisation'	$\in \{1.5, 2.0, 4.0\}$
		2.0
		2.0

*For a scenario analysis of the marked parameters see Appendix D

We assume Euclidean distances d_{ij} between the midpoints of patches i and j , i.e. the distance d_{ij} between patches (x_i, y_i) and (x_j, y_j) is $d_{ij} = \sqrt{(x_i - x_j)^2 + (y_i - y_j)^2}$. Without loss of generality, we assume a distance of one for the eight nearest patches, equalling the minimum dispersal distance of the target species.

Each patch in the landscape can potentially serve as a habitat for a target species under two conditions. First, it needs to be climatically suitable. This means, the time-dependent climate suitability value of a patch, which determines to what degree the target species can find suitable habitat on the patch, needs to exceed a certain threshold value. Second, conservation measures are carried out on a patch i in a specific time step t ($c_{i,t}^{cons} = 1$). This causes opportunity costs of conservation OC_i that are assumed to be constant over all time steps. If no conservation measures are carried out ($c_{i,t}^{cons} = 0$) the patch may be used for economic purposes, e.g. intensive agricultural production, and no conservation costs arise.

Opportunity costs of conservation are spatially heterogeneous and follow a random distribution within a range of $[\overline{OC} - \sigma_{OC}, \overline{OC} + \sigma_{OC}]$, where σ_{OC} is the standard variation and \overline{OC} the mean conservation costs which equal 1.

2.3 Climate Change

Our modelling of climate change is based on Hily et al. (2017) and is adapted slightly to fit our simulation model. We assume that in our model landscape, climatic conditions differ according to the relative north–south location of a particular patch. We assign a climate suitability value $cs_i(t) \in [0, 1]$ to each patch in the landscape, representing the probability with which habitat is provided if that patch is under conservation. To keep our model simple, we do not explicitly model (local) climatic conditions by e.g. modelling precipitation or temperature, but instead model habitat suitability directly. In this context, $cs_i(t)$ is a dimension-less value representing habitat quality and thus the probability by which a habitat is potentially provided on a conserved patch. We assume that the climate suitability of a patch $cs_i(t)$ changes in every time step t , and thus provides different habitat conditions for the target species over time. We assume the climate suitability to follow a general bell-shape, such that

$$cs_i(t) = \exp\left(\frac{-(j - \mu_t)^2}{2 \times \rho^2}\right) \quad (1)$$

with $\mu_t = \rho + t \times \frac{j-2 \times \rho}{T}$ being the centre of the climate suitability bell curve at time step $t \in [1, 100]$, ρ an indicator for the bell shape's curvature, and j the y-coordinate of patch i . The bell-shaped climate suitability distribution in the landscape moves through the landscape from south to north (Fig. 2b).

The introduction of a climate suitability threshold cs^{thr} generates a climatically suitable zone (CSZ), containing all patches in the landscape that are suitable for a target species' habitat. A patch provides suitable habitat for a target species only if the climate suitability of a patch at a specific point in time is larger than a threshold value ($cs_i(t) > cs^{thr}$). Taking a small (large) value of cs^{thr} implies that a large (small) CSZ exists, and allows the target species to colonise patches with low (high) climate suitability and the conservation agency to set respective patches under conservation. The CSZ moves through the landscape from

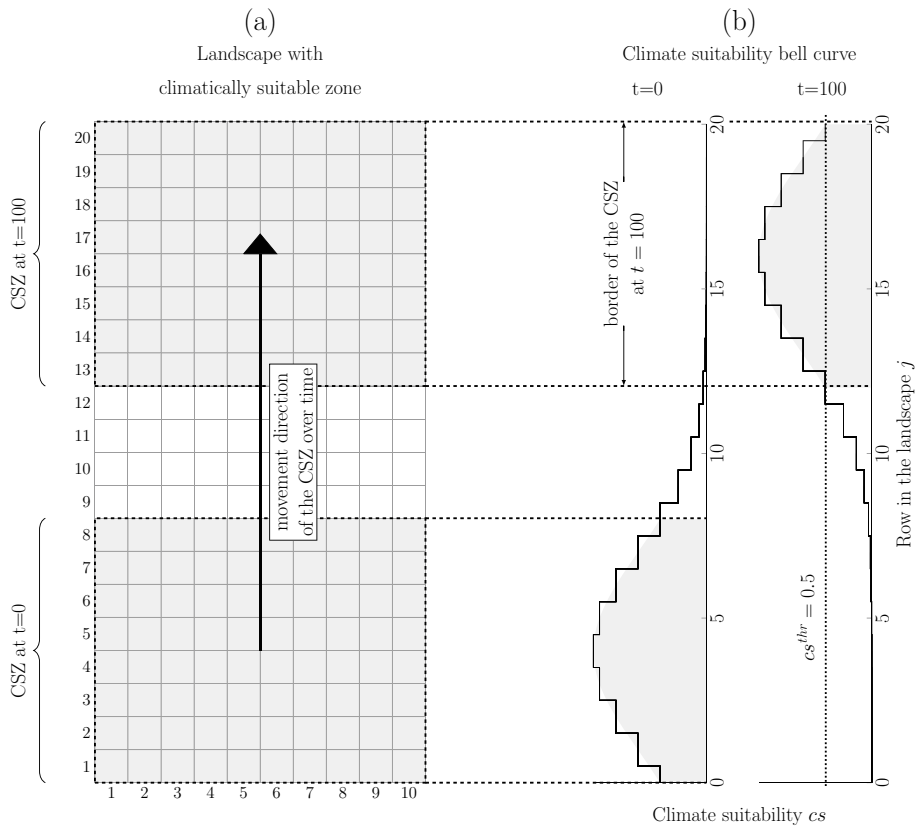


Fig. 2 **a** Spatially explicit landscape consisting of 10×20 patches including the climatically suitable zone (CSZ, shaded area) at time steps $t = 0$ and $t = 100$, **b** climate suitability bell curves according to Eq. (1) in their respective base case parametrisation (see Table 2) and climate suitability threshold $cs^{thr} = 0.5$, leading to the CSZ at the different time steps $t \in \{0, 100\}$. The shaded area and the corresponding borders represent the CSZ at time steps $t = 0$ and $t = 100$

south to north over time, implying that the target species can only survive if it relocates northwards.

Each patch in the landscape will only remain within the CSZ for a specific number of time steps between entering the CSZ at its northern edge, and falling out of the southern edge of the CSZ. In the base case parametrisation, a patch will stay in the CSZ for 6 time steps. The length of this time period (i.e. the number of time steps) depends on the width of the CSZ, i.e. on the bell-shape defining parameter ρ and the climate suitability threshold cs^{thr} . The time span it takes for the CSZ to pass over a patch also depends on the climate change speed T , i.e. the overall number of time steps simulated.

2.4 Ecological Dynamics

Regarding the ecological dynamics, we are primarily interested in the migration of a target species in a landscape under climate change and assume this species will populate the landscape and colonise new patches according to metapopulation dynamics. In order to model these dynamics, we take the metapopulation model by Hanski (1999; chapter 5), which is frequently used in comparable generic models (e.g. Donaldson et al. 2021; Drechsler 2021; Nicholson et al. 2006; Mestre et al. 2017). The metapopulation model considers species characteristics and ecological processes (dispersal distance, emigration rate, immigration rate, and local extinction) to model the colonisation and extinction processes in the landscape (but it neglects other aspects such as patch-level resources and reproduction dynamics). We modify Hanski's metapopulation model by including climate aspects to take into account climate change. Given the already high complexity of our ecological-economic model, and similar to Hily et al. (2017) and Drechsler (2021), we ignore ecological dynamics like multi-species interactions, as well as spatially heterogeneous local population density, as such considerations would require adding another level of complexity without contributing much to our aim of understanding the movement of species in a landscape whose dynamics are driven by climate change.

The target species can inhabit patches, if these are under conservation, i.e. $c_i^{cons}(t) = 1$, and located within the CSZ, i.e. have a climate suitability $cs_i(t) \geq cs^{thr}$ (cf. Alagador et al. (2014 and 2016) for a discussion of patch habitability depending on conservation status and climate suitability). By migrating from an occupied patch i to an unoccupied patch j , the target species can colonise new habitat over time. Irrespective of migration, the target species also faces a probability of local extinction $e_i(t)$ on each patch i

$$e_i(t) = 1 - 0.9 * cs_i(t) \quad (2)$$

which is negatively correlated with time dependent climatic suitability $cs_i(t)$ and is independent of local immigration and emigration processes.

The species migration dynamics are governed by the rate of emigration (ν) from all colonised patches and the immigration rate into all patches i that can in principle be colonised in time step t ($Im_{i,t}$). The original Hanski model contains a positive correlation between habitat area size and maximum local population of a patch and thus local extinction probability $e_i(t)$ and emigration rate ν (see Hanski 1999; chapter 5.3), absent of any further local population density relations. The metapopulation approach in our model abstracts from spatially heterogeneous local populations and density considerations, as we assume that all patches are of equal size and are populated with the maximum local population (if colonised). This results in a constant emigration rate ν for all patches in the landscape. The implicit upper population boundary of all patches represents local factors like resource availability and limits to reproduction.

The immigration rate $Im_{i,t}$ depends on the combined immigration into a patch i from all other patches k within the dispersal distance δ of the target species at time step t and is modelled as follows:

$$Im_{i,t} = \sum_{k=1}^K h_k(t) * \nu * \frac{\exp(-d_{i,k}/\delta)}{s(t)}. \quad (3)$$

Overall, K patches are located within the CSZ, and every patch $k \in K$ occupied at time step t (indicated by the binary variable $h_k(t)$) contributes to the local immigration

by its emigration rate v . The probability of emigrating individuals successfully reaching any patch i in the landscape, $\exp(-d_{i,k}/\delta)$, decreases with increasing distance $d_{i,k}$ between patches k and i , and depends on the target species' dispersal distance δ (i.e. the maximum distance a species can travel in one time step). Since the target species splits its emigration efforts equally over all climatically suitable patches within the dispersal distance of patch k , we have to also consider the number of these patches, $s(t)$.

Based on the immigration rate $\text{Im}_{i,t}$, and according to Hanski (1999; chapter 5.3) we calculate the probability for successful colonisation of a patch i , i.e. $\tau_i(t)$, as

$$\tau_i(t) = \begin{cases} \frac{(\text{Im}_{i,t})^2}{(\text{Im}_{i,t})^2 + \theta^2} & \text{if } cs_i(t) \geq cs_{thr} \text{ and } c_i^{cons}(t) = 1 \\ 0 & \text{otherwise} \end{cases} \quad (4)$$

where θ represents a threshold level of immigration necessary for successful colonisation of any not colonised patch. For a detailed explanation of the ecological assumptions underlying Eq. (4), see Hanski (1994, 1999).

As the CSZ shifts northwards over time, the climate suitability of patches at the southern end of the CSZ eventually falls below the climate suitability threshold cs_{thr} and thus patches become unsuitable for the species, eventually leading to definite local extinction.

The colonisation and extinction processes generate dynamics in the metapopulation model over the model time frame T (i.e. 100 time steps), within which changing climate conditions can be considered as a driving factor behind local extinction. Taking into account the inherent stochasticity of the model, we employ a Monte Carlo simulation with 2000 simulation runs for each particular model parametrisation.

Finally, we calculate the landscape level extinction rate of the species population at the landscape level as the share of simulation runs within a particular model parametrisation in which the target species goes extinct in the whole landscape before the end of the simulation time frame T . This landscape level extinction rate is then used as an indicator for the conservation performance in our model. Low landscape level extinction rates indicate a superior conservation performance in comparison to high landscape level extinction rates.

2.5 Decision Problem of the Conservation Agency

The generic target of the conservation agency is to pursue a conservation objective cost-effectively, i.e. to maximise conservation performance with given financial resources (Wätzold and Schwerdtner 2005). We select the landscape level rate of species extinction at the end of the simulation timeframe as an indicator to measure the performance in terms of obtaining the conservation goal (see Sect. 2.4). In order to reach the desired conservation goal, the conservation agency implements certain conservation measures in the landscape. In this context, we assume that the agency is fully informed about the colonisation status of every patch (colonised or not colonised) and the climate suitability of each patch in any time step. The agency chooses between two governance modes: (1) buy land and implement conservation measures itself (*buy alternative*), or (2) pay landowners for their voluntary provision (*compensation alternative*) of equally designed conservation measures. The agency has to choose one of the alternatives – a combination of the two governance modes is not feasible. For the implementation of conservation measures, the agency has to develop a patch selection strategy to decide which patches to conserve. We consider four strategies for each of the two governance modes resulting in eight governance mode—patch selection

strategy pairs. In the following, we first introduce the budget available for covering conservation costs and its allocation over time. We then explain how we model the two governance modes and the corresponding budget equations, before we finally describe the four patch selection strategies.

2.6 Budget Comparability

The implementation of conservation measures within a certain governance mode—patch selection strategy combination incurs costs, which are covered by the agency's budget. To apply the cost-effectiveness criterion, budgets in all governance mode—patch selection strategy combinations have to be comparable. To achieve this, we assume that the present values of the eight individual cost-streams are equal, which enables us to compare their conservation performances and thus assess changes in the cost-effectiveness of the governance mode—patch selection strategy pairs due to changes in the model parametrisation.

It is necessary to assume equal present values for budgets across governance mode—patch selection strategy pairs, because all eight governance mode—patch selection strategy pairs generate different amounts of costs at each time step, as each patch selection strategy requires the purchase of different patches in the landscape or the compensation of landowners. Generally, high initial costs arise for land purchase, while relatively high recurring costs incur for compensation. We thus assume that the discounted sum of all arising costs, the present value, has to be equal for all cost streams. The available budgets in each governance mode—patch selection strategy pair can thus differ for each time step allowing for the specific governance mode—patch selection strategy pair's needs, while still being comparable in present value terms with all other governance mode—patch selection strategy pairs. The relation of present values (PV) of the respective budgets, $PV(B^{buy}) = PV(B^{comp})$, translates into:

$$PV(B^{buy}) = \sum_{t=0}^T B_t^{comp} \times (1+r)^t. \quad (5)$$

$$B_t^{comp} = \frac{-r \times (B^{buy} \times r^T - \epsilon)}{1 - r^{T+1}}, \quad (6)$$

with B^{buy} and B^{comp} being the budget available for patch purchase and landowner compensation, T the length of the total timeframe, r the interest rate, and ϵ the residual budget at the end of period T . Because a different set of patches is conserved in each time step t in the *compensation alternative*, the available budget in time step t is likely not covering the expenses exactly, but a small residual budget remains. This budget is then transferred to the next time step $t+1$, where it complements the available budget. In the last time step T , this residual budget cannot be transferred, and thus the present value of the total compensation cost stream has to be corrected by this amount ϵ , which is therefore subtracted in Eq. 6.

The whole budget is available at the beginning of time step $t=0$ for the *buy alternative*. For the *compensation alternative*, we assume that B_t^{comp} is set so that in each time step t an equal monetary amount (compensation annuity) is available to the agency to spend, i.e. c_t^{comp} of Eq. 9 (for a detailed explanation, see Appendix D). The conservation agency conserves as many patches as possible for a given budget in a certain period t . Any leftover budget at the end of a period is transferred to the next period and added to

the respective budget, including interest. We assume that the conservation agency does not know the individual costs of conservation for a particular patch. Like Wätzold and Drechsler (2014) we assume that the agency however has information about the uniform random distribution of costs in the landscape.

2.6.1 Buy Alternative

The *buy alternative* characterises the agency's option to purchase and consecutively manage patches for conservation. The costs of an individual patch purchase are defined as

$$c_i^{buy} = p_i^{buy} + tc_i^{buy}, \quad (7)$$

with $p_i^{buy} = \overline{p^{buy}} \pm \sigma_{p^{buy}}$ being the uniform randomly distributed purchasing price, $\overline{p^{buy}} = \frac{OC}{r}$ the mean purchasing price of patches in the landscape, $\sigma_{p^{buy}} = \sigma_{OC} \times \overline{p^{buy}}$ the standard deviation of purchasing prices, \overline{OC} the mean conservation costs, r the interest rate, and σ_{OC} the standard deviation of conservation costs. Transaction costs for purchasing a patch $tc_i^{buy} = \overline{tc^{buy}} \pm \sigma_{tc}$ (such as notary fees, contract negotiation costs, etc.) are uniformly randomly distributed. For simplicity, we assume that patch prices do not change over time.

The conservation agency is able to purchase new patches as long as the remaining budget is high enough. The agency is not allowed to have negative budgets, i.e. taking loans to fund patch purchase. We assume myopic spending behavior on the part of the agency, thus strategically saving budget for later periods is not allowed. Purchased patches are managed in the prescribed conservation sense. Following Schöttker et al. (2016) we assume that the costs of managing patches are equal to potential income generated from these measures, and hence we only need to consider the costs of purchasing patches in the *buy alternative*.

Depending on the chosen patch selection strategy species monitoring costs might occur (cf. de Vries and Hanley 2016). These are recurring monitoring costs of $mc_i = \overline{mc} \pm \sigma_{mc}$ per patch in each time step, with \overline{mc} the mean monitoring costs and σ_{mc} the variation bandwidth. Monitoring costs are initially drawn randomly, like transaction costs, from a uniform distribution (according to \overline{mc} and σ_{mc}) and do not change over time.

After a patch i is purchased, it is set under conservation, resulting in habitat generation on this patch if climatic conditions for the target species on that patch are good enough, i.e. $cs_i(t) \geq cs^{thr}$. Patch purchase then results in $c_i^{cons}(t) = 1$.

We assume that in all four patch selection strategies the agency only purchases patches within the CSZ as $cs_i(t) < cs^{thr}$ for all patches outside the CSZ. We also assume that if a previously purchased patch falls out of the CSZ after some time due to climate change, the conservation agency sells that patch and receives the amount

$$c_i^{sell} = p_i^{sell} - tc_i^{sell}. \quad (8)$$

Following from the assumption that purchasing prices do not change over time, the conservation agency receives the same amount from selling a patch as it paid for its acquisition ($p_i^{sell} = p_i^{buy}$). However, it has to bear the transaction costs, which are assumed to be equal for patch purchase and sale ($tc_i^{sell} = tc_i^{buy}$).

2.6.2 Compensation Alternative

In the *compensation alternative*, the conservation agency does not purchase areas for conservation. Instead, it offers a compensation payment to landowners to incentivise them to implement conservation measures voluntarily (equivalent to the measures in the *buy alternative*) on their land. Compensation payments are spatially homogeneous and equal the highest opportunity costs $oc(t)$ of any landowners participating in the compensation alternative at time step t .

For each patch under conservation, the conservation agency has to pay

$$c^{comp}(t) = oc(t) + tc^{comp}(t) \quad (9)$$

in period t , resulting in a periodical payment subtracted from the budget at each time step, with $tc^{comp}(t)$ being the transaction cost per time step for setting up and implementing a conservation measure (such as patch finding costs, contract negotiation, etc.).

After a patch is set under conservation ($c_i^{cons}(t) = 1$), it remains in that state for one time step. At the next time step, the conservation agency renegotiates conservation contracts. Depending on the patch selection strategy, the agency might want to keep certain patches under conservation for more than one time step, or to alter the conservation location according to its priorities (see Sect. 2.6.3).

Comparable to the *buy alternative*, the agency also chooses potential conservation areas only within the CSZ. Hence, $cs_i(t) \geq cs^{thr}$ for all patches under conservation. The periodically renewed conservation decision of the agency results in potentially varying locations of patches under conservation.

2.6.3 Patch Selection Strategies

To implement conservation measures, the conservation agency has to identify suitable patches. We consider four different patch selection strategies for this purpose ('price prioritisation', 'species abundance prioritisation', 'climate suitability prioritisation', 'climate change direction prioritisation'). The first patch selection strategy is motivated purely by cost concerns, whereas patch selection strategy 2–4 follow the notion that prioritisation and spatial coordination of potential habitats based on natural processes and characteristics (e.g. species abundance and general climate-related suitability of potential habitats), may increase species survival (cf. Alagador et al. 2016) and thus the cost-effectiveness of conservation (Albers et al. 2006; Reside et al. 2019).

(1) 'Price prioritisation' characterises a patch selection strategy in which the conservation agency prefers low-cost patches over more expensive ones. With the *buy alternative* this means that the agency buys the available least cost patches in the CSZ. With the *compensation alternative*, the patches with the lowest compensation payment requests are added to the conserved patches (Fig. 3a). The resulting conservation patches are not necessarily connected to each other, so that a target species might not successfully migrate between all patches under conservation. This potentially inhibits colonisation, but will generate the highest number of patches under conservation for a given budget.

(2) For the patch selection strategy 'species abundance prioritisation' the conservation agency only buys or compensates patches that are within the dispersal distance of colonised patches (Fig. 3b). This generates a cluster of conserved patches around existing habitat and leads to connected areas for the target species to colonise. However, as not all patches are available for conservation, more expensive patches might have to be added, leading to a

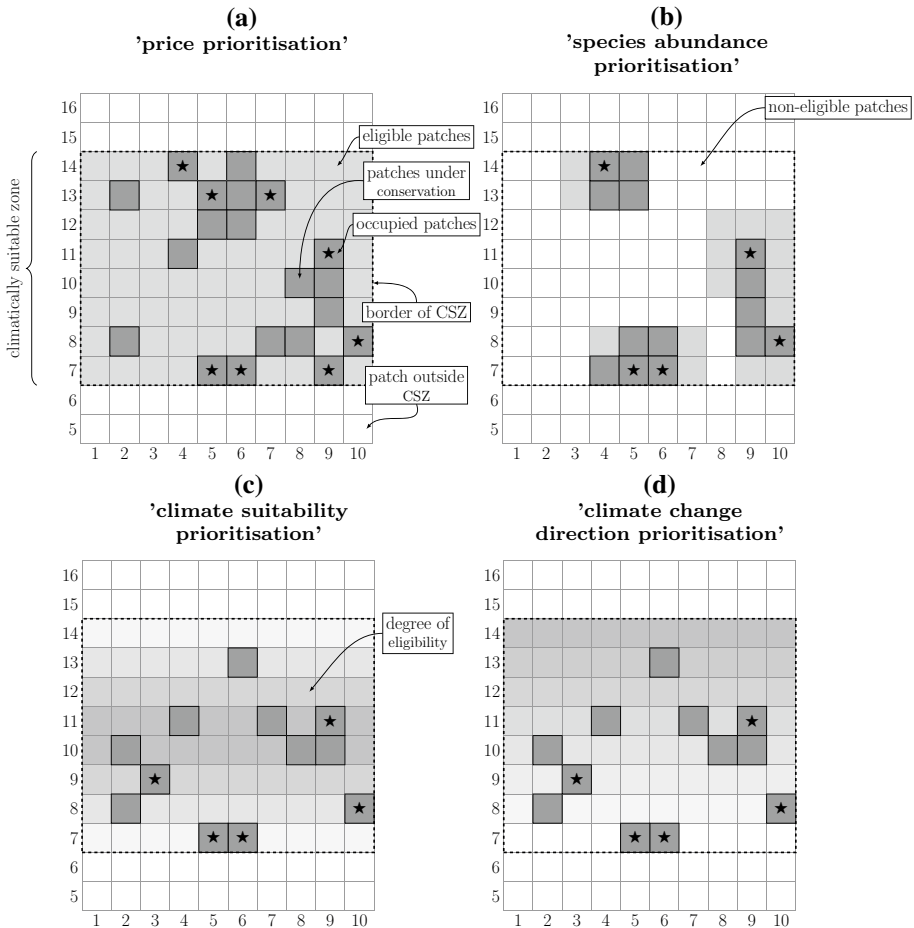


Fig. 3 Visualisation of the four different patch selection strategies and the corresponding patch location. **a** 'Price prioritisation' allows for patch selection in the complete CSZ, only depending on the purchase price or compensation costs. **b** 'Species abundance prioritisation' only selects patches within the dispersal distance of already occupied patches. **c** 'Climate suitability prioritisation' prefers patches with higher climate suitability over patches with lower climate suitability, and **d** 'Climate change direction prioritisation', prefers patches at the northern end of the CSZ over patches at the southern end of the CSZ

lower number of conserved patches than with the patch selection strategy 'price prioritisation'. Due to the need to identify colonised patches in this patch selection strategy, monitoring costs of $mc_i = \overline{mc} \pm \sigma_{mc}$ arise for the agency at each time step.

(3) We assume that the conservation agency has full information about the climate suitability of all patches in the landscape. The patch selection strategy 'climate suitability prioritisation' prefers patches with a high climate suitability (Fig. 3c), specifically, patches in the centre of the climate suitability bell curve, as here the climate suitability value is highest. However, if costs are sufficiently low, more northern or southern patches can also be selected, allowing for a spatial spread of the conserved patches over the CSZ. By introducing a scaling factor λ (Eq. 8), we are able to foster or loosen this prioritisation and allow the agency to either almost exclusively focus on the most centred patches (high λ), or allow

a broader spread of patches as (for given climate suitability) less expensive but further away patches are selected (low λ). In order to include costs in this patch selection strategy, we introduce the “suitability price” of each patch, which is a non-homogeneous payment, depending on a combination of the climate suitability of a patch and its opportunity costs. The “suitability price” includes both the (normalised) price and the (normalised) climate suitability of that patch as follows:

$$p_i^{suit} = p_i^{norm} + cs_i^{norm}(t) \times \lambda, \quad (10)$$

with p_i^{norm} the price of patch i normalised on a scale of 0 to 1 (in which the lowest patch price in the landscape is 0 and the most expensive price is 1), $cs_i^{norm}(t)$ the normalised climate suitability of patch i and λ the scaling factor. Instead of using only the price for patch selection (as in the patch selection strategy ‘price prioritisation’), the suitability price is now used as a selection criterion. Obviously, we use the regular price with respect to budgetary calculations.

(4) Due to the CSZ’s movement in a northern direction over time, already selected and colonised patches move to the southern edge of the CSZ. By assuming that the conservation agency has full information about the direction of climate change, we can design a fourth patch selection strategy in which the agency prioritises patches closer to the northern edge of the CSZ (Fig. 3d). Due to the northward movement of the CSZ, these patches will stay in the CSZ for a long time. The resulting conserved patches are comparable to the ones under the ‘climate suitability prioritisation’ but biased towards northern patches. By introducing a scaling factor κ into this patch selection strategy, we can vary the agency’s prioritisation strength and allow for a more or less strict patch selection close to the northern edge of the CSZ. Similar to the patch selection strategy ‘climate suitability prioritisation’, we calculate a “suitability price” for each patch, which includes both the (normalised) price and the (normalised) climate suitability of that patch and represents a non-homogeneous payment to the individual landowners:

$$p_i^{suit} = p_i^{norm} + csz_i^{row}(t) \times \kappa, \quad (11)$$

with p_i^{norm} the price of patch i normalised on a scale of 0 to 1 (in which the lowest patch price in the landscape is 0 and the most expensive price is 1), and $csz_i^{row}(t)$ the normalised row number in which a certain patch i is located within the CSZ (more northern patches have higher row numbers and thus higher $csz_i^{row}(t)$ leading to the intended prioritisation).

3 Analysis

For model analysis we apply a Monte Carlo simulation, in which each parameter set—i.e. selected combinations of parameters specified in Table 2—is simulated 2000 times to allow an analysis of the whole bandwidth of potential outcomes and to avoid randomly extreme results resulting from the model’s inherent stochasticity. A simulation run refers to one single calculation of the model for one parameter set.

The parameters cs^{thr} , ρ , m_t , and θ influence the shape of the climate bell curve, and thus potentially have an effect on both governance modes and all patch selection strategies. In contrast, λ and κ affect the prioritisation strength of the two climate-sensitive patch selection strategies, and hence may only influence the outcome of these patch selection strategies. The economic parameters OC , tc^{buy} , and \overline{mc} impact the different cost measures, while

the interest rate r is used for discounting and budget calculations in all governance mode—patch selection strategy pairs. σ_{OC} , σ_{tchuy} , and σ_{mc} determine the range of all randomly drawn cost parameters in the simulation. The ecological parameters ν and δ influence the dispersal ability of the target species affecting the ecological dynamics in all governance mode—patch selection strategy pairs.

We calculate a reference base case with a corresponding base case parametrisation. The selection of parameter values can be seen as a compromise between values that resemble to some extent economic, ecological, and climatic conditions in the real world, values taken in similar models, and the need to take into account restrictions in terms of computing time (for example by choosing a rather small landscape size). By its very nature, the purpose of a conceptual model is to enhance the understanding of relationships between changes in model parameters and model output, not to provide information for a specific landscape, cost structure, species, and climatic conditions. We therefore paid particular attention to selecting appropriate relationships. For example, while mean conservation costs were normalised to one, transaction costs were selected to represent 10% of conservation costs (representing a reasonable proxy for many real world cases), and the dispersal distance was selected so that a species can reach part of the landscape (approximately 4%) but not the whole landscape (representing a species which needs some degree of habitat connectedness for its long term survival). In Table 2 we briefly indicate the motivation for the selection of each parameter value.

After calculation of the reference base case, we individually vary climate related parameters in specified ranges to values lower and higher than the base case value to identify the impact of each parameter on the cost-effectiveness of each governance mode—patch selection strategy pair (sensitivity analysis).

4 Results

We start the presentation of our results by identifying general effects that potentially influence the cost-effectiveness of the governance mode—patch selection strategy pairs. We then present the results of sensitivity analyses in which climatic model parameters are varied individually.

4.1 Identification of General Effects

Analysis of the results revealed five effects influencing the cost-effectiveness of each governance mode—patch selection strategy pair. Wätzold and Drechsler (2014) have already identified two of the effects—the *patch restriction effect* and the *connectivity effect*. The remaining three effects—the *climate prioritisation effect*, the *adaptability effect* and the *climate migration effect*—are newly identified in this work.

- (1) The *patch restriction effect* exists due to restrictions on eligible patches if connected habitat requirements or climate suitability restrictions are to be met by a specific governance mode—patch selection strategy pair. In these cases, more costly patches are most likely to be selected compared to a situation in which the conservation agency

can freely choose patches in the whole CSZ. Therefore, a restriction of eligible patches tends to increase conservation cost and reduce cost-effectiveness.

- (2) The *connectivity effect* occurs if improved connectivity of conserved patches improves the conservation performance, and thus the cost-effectiveness.
- (3) The *climate prioritisation effect* leads to improved ecological conditions of patches under conservation as they are chosen in climatically more suitable areas within the CSZ, and increases cost-effectiveness.
- (4) The *adaptability effect* exists because the adaptation of the conservation network to changing climatic conditions can be fast or slow. This adaptation possibility allows for a flexible selection of suitable patches and hence improves the conservation performance, and thus cost-effectiveness.
- (5) The *climate migration effect*: As the CSZ moves northwards over time, selected patches within the CSZ move closer to its southern edge until they eventually drop out of the CSZ and are either sold or taken out of compensation. The conservation agency is then able to select new patches within the CSZ according to the four different patch selection strategies. The *climate migration effect* arises if patches are selected according to climatic conditions and hence the conservation network has a strong east–west orientation, i.e. new conservation happens mainly at the northern edge of the CSZ. This, however, leads to fewer conserved patches within the rest of the CSZ, making species migration within the landscape more difficult. The *climate migration effect* thus leads to increased extinction and reduced cost-effectiveness due to the strong spatial correlation of newly selected patches (cf. Albers et al. 2016) resulting in a lack of connectedness with existing patches.

In the following, we use the five effects to explain the changes in cost-effectiveness of the eight governance mode—patch selection strategy pairs. In our analysis, we ignore governance mode—patch selection strategy pairs in which parameter variations cause no or only very minor changes in cost-effectiveness (see Section D in the Appendix) as such changes might be caused by the general stochasticity of the model. Table 3 summarises the results.

4.2 Scenario I: Climate Change Speed

The cost-effectiveness of three governance mode—patch selection strategy pairs is influenced by variations in climate change speed, i.e. variations in the overall simulation timeframe T . A short timeframe (small T) represents fast climate change as it takes fewer time steps for the climate suitability to vary and the CSZ to move across the landscape (Fig. 4).

For the ‘price prioritisation’ strategy (Fig. 4a), we find that the cost-effectiveness of the *compensation alternative* decreases with increasing climate change speed. We explain this result with the combination of a generally reduced ecological suitability of the landscape for the target species due to a faster patch turnover because of increased climate change speed and a low *connectivity effect* due to patch location according to costs. In contrast to other patch selection strategies, the *adaptability effect* does not play a role in the ‘price prioritisation’ strategy as the conserved patches are selected only according to the patch prices without explicit adaptation according to changing climatic conditions.

Increasing climate change speed, however, increases the cost-effectiveness of the ‘species abundance prioritisation’ strategy for the *buy alternative* (Fig. 4b). We explain this observation as follows. At the time of purchase, patches are near existing species

Table 3 General influence of the individual effects on the cost-effectiveness of the governance mode—patch selection strategy pairs with (a) increasing climate change speed, (b) increasing climate suitability threshold and (c) increasing climate change direction prioritisation strength. + indicates a positive effect, —a negative effect on the cost-effectiveness of the governance mode—patch selection strategy pair. 0 indicates that no influence could be attributed to a particular effect. governance mode—patch selection strategy pairs whose cost-effectiveness does not change are not shown

Governance mode		Patch selection strategy		Effect					
				Total effect	Patch restr. effect	Connectivity effect	Climate prio. effect	Adaptability effect	Climate migration effect
(a) Increasing climate change speed	Buy		<i>Species abundance prio</i>	+	0	+	0	0	0
			<i>Climate change direction prio</i>	–	0	0	0	0	–
	Compensate	Buy	<i>Price prio</i>	–	0	–	0	+	0
			<i>Price prio</i>	+	–	+	0	0	0
(b) Increasing climate suitability threshold	Buy		<i>Species abundance prio</i>	+	0	+	0	0	0
			<i>Climate change direction prio</i>	+	0	+	+	0	0
	Compensate	Buy	<i>Price prio</i>	+	–	+	0	+	0
			<i>Climate change direction prio</i>	–	0	–	0	0	–
(c) Increasing climate change direction prioritisation strength	Buy		<i>Species abundance prio</i>	+	0	+	0	+	0
			<i>Climate change direction prio</i>	–	0	–	0	0	–

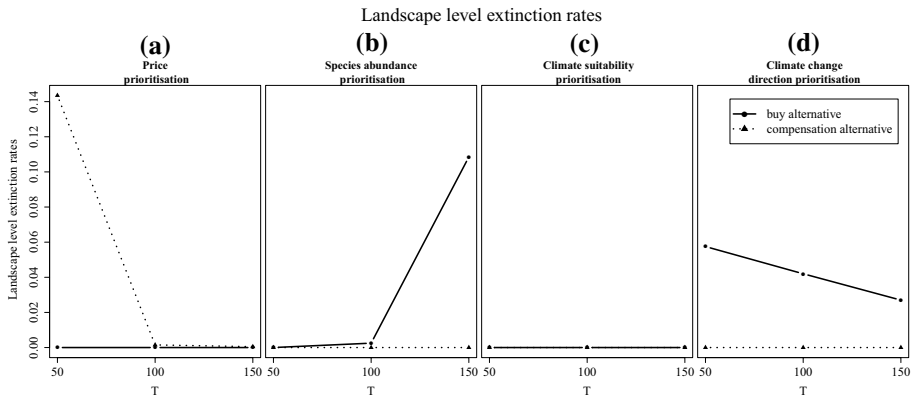


Fig. 4 Changes in landscape level extinction rates due to changes in maximum length of the simulation timeframe T, (i.e. climate change speed decreases with increasing T). **a–d** represent the landscape level extinction rates for all four strategies in the buy and compensation alternative

populations. However, they may lose this connection due to extinction processes, resulting in a decreased value for conservation. Fast climate change implies that these patches cease to be in the CSZ within a relatively short timeframe, which enables a fast re-allocation of these patches close to species populations (combination of *adaptability effect* and *connectivity effect*). This results in improved cost-effectiveness.

We do not observe any influence of changing climate change speed on the cost-effectiveness in the ‘climate suitability prioritisation’ strategy in any of the two governance modes (Fig. 4c). However, we find faster climate change speed increases landscape level extinction rates in the ‘climate change direction prioritization’ strategy for the *buy alternative* (Fig. 4d), which reduces its cost-effectiveness. We explain this result with a combination of a generally reduced ecological suitability of the landscape for the target species due to a faster patch turnover and the occurrence of the *climate migration effect* in the whole CSZ, which does not lead to well-connected patches.

4.3 Scenario II: Climate Suitability Threshold

Changes in the climate suitability threshold value cs^{thr} influence the cost-effectiveness of four governance mode—patch selection strategy pairs (Fig. 5). For all of these changes, it is important to note that the climate suitability threshold cs^{thr} determines the width of the CSZ, which impacts the *connectivity effect* and the *patch restriction effect*, both of which weaken with an increasing CSZ respectively a low cs^{thr} . We generally find that with increasing CSZ size (decreasing cs^{thr}) the cost-effectiveness decreases, suggesting that the negative influence of reduced connectivity (*connectivity effect*) is stronger than the positive influence of increased patch eligibility (*patch restriction effect*).

A strong negative effect on cost-effectiveness can be observed for small values of cs^{thr} (large CSZ), in the ‘climate change direction prioritisation strategy’ (Fig. 5d) for the *buy alternative*. This can be explained by the additional occurrence of the *climate prioritisation effect* in this patch selection strategy, which leads to even less connectivity compared to the other patch selection strategies.

Generally, *compensation alternative* strategies perform well even with large CSZs because of the strong *adaptability effect*, the exception being the ‘price prioritisation

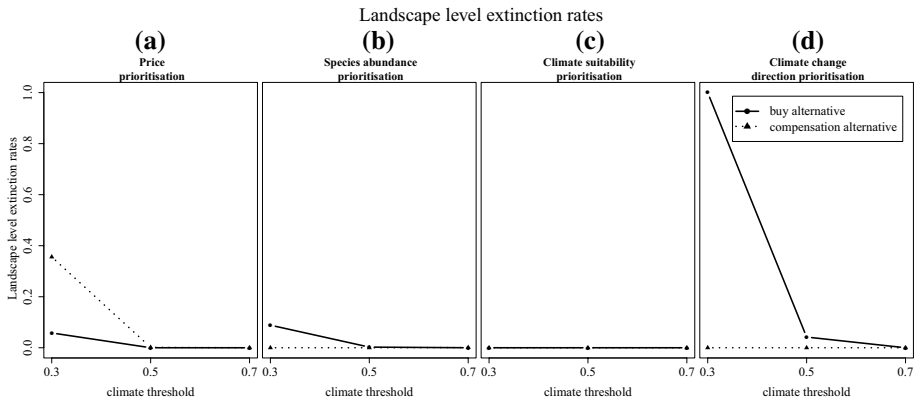


Fig. 5 Landscape level extinction rate of the different governance mode—patch selection strategy pairs with changing climate threshold, resulting in changing CSZ sizes

strategy’, in which the *adaptability effect* is not relevant as patch selection is only driven by prices.

4.4 Scenario III: Strength of Climate Prioritisation

Within the patch selection strategies ‘climate suitability prioritisation’ and ‘climate change direction prioritisation’, patch selection takes place according to either climate suitability or climate change direction. We introduced scaling factors λ and κ for the strategies to define the strength of prioritisation of respective patch selections. A higher λ (κ) results in a stronger prioritisation for climate suitability (climate change direction) relative to patch prices. Changes in λ only affect the ‘climate suitability prioritisation strategy’, and changes in κ only affect the ‘climate change direction prioritisation strategy’. The ‘price prioritisation strategy’ and the ‘species abundance prioritisation strategy’ remain unaffected, as neither parameter alters their respective patch selection mechanism.

We found that changes in κ only show an influence on the cost-effectiveness of the ‘climate change direction prioritisation strategy’ for the *buy alternative* (see Fig. 6d). High values of κ (strong prioritisation for climate change direction) result in decreased cost-effectiveness compared to lower values of κ due to a decreasing *connectivity effect* and an increasing *climate migration effect*. With increasing κ , newly added patches are predominantly located in the most northern part of the CSZ resulting in an increasing number of unconnected patches in the CSZ.

4.5 Scenario IV: Shape of the Climate Suitability Bell Curve

We find only negligible effects of variations in ρ (curvature of the climate suitability bell shape) on the cost-effectiveness of the governance mode—patch selection strategy pairs (see Fig. A13 in Appendix D). This might be because changes in the curvature of the bell shape are not necessarily very strong within the CSZ and only have marginal effects on CSZ size. This results in negligible effects on governance mode—patch selection strategy pair’s performances.

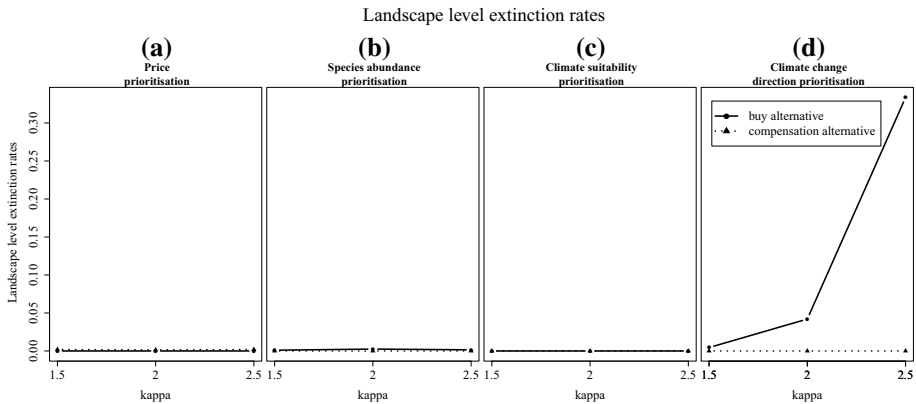


Fig. 6 Influence of changes in κ on the landscape level extinction rate in the buy alternative and the compensation alternative for each of the four patch selection strategies

5 Summary and Discussion

The purpose of this paper was to analyse the impact of changes in climatic parameters on the cost-effectiveness of different governance modes and specific patch selection strategies with a conceptual model. We assume that conservation agencies have two alternative governance modes to select. (1) Buy conservation areas and implement conservation activities on this land (*buy alternative*), and compensate private landowners for their voluntary provision of conservation measures on their own land (*compensation alternative*). We further assume that the conservation agency chooses from four patch selection strategies. (1) Select the least cost patches in the landscape ('price prioritisation'), (2) select patches close to areas already populated by a target species ('species abundance prioritisation'), (3) select patches with the highest climate suitability ('climate suitability prioritisation'), and (4) select patches that remain climatically suitable for the longest time ('climate change direction prioritisation').

We wish to highlight the following three general key insights. First, buying areas for conservation produces a relatively rigid spatial selection of conserved patches due to the long-term commitment for certain conservation areas within the landscape. While a rigid patch location has a positive impact on species due to reduced habitat turnover, it does not allow swift adaptation to changing climatic conditions. In contrast, the *compensation alternative* is more flexible, i.e. patches are potentially changing their conservation status more often as compensation contracts are typically only valid for short time periods. More specifically, differences in adaptability result in a higher possibility of the *compensation alternative* to adapt to changing conditions, and thus to being a more robust choice against uncertain and changing climatic conditions than the *buy alternative* (Drechsler 2020; Gerling and Wätzold 2021; Hamaide et al. 2014).

Second, we find that against the presence of changing climatic conditions, the cost-effectiveness of governance modes strongly depends on the choice of patch selection strategy. However, as the performance of a specific patch selection strategy depends on the present climatic conditions, the optimal choice of a governance mode—patch selection strategy pair also depends on present climatic conditions. Within the range of analysed parameters, we find a weak indication that the *buy alternative* has a cost-effectiveness advantage when focusing on the least cost conservation sites, disregarding climatic conditions in the patch

selection process (i.e. applying the ‘price prioritisation strategy’). In contrast, landowner compensation tends to have an advantage with more specific patch selection strategies (i.e. the ‘species abundance prioritisation’, ‘climate suitability prioritisation’ or ‘climate change direction prioritisation’ strategy). We explain this with the advantages in terms of adaptability of the *compensation alternative*. Here, a more specific site selection by prioritising either ecological or climatic characteristics has a stronger influence than in the *buy alternative* and, hence, price prioritisation is comparatively less relevant.

Third, conservation agencies may prioritise conservation areas that are located at the northern edge of the CSZ and are therefore within the CSZ for a long time (i.e. choose the ‘climate change direction prioritisation’ strategy). In this case, however, a trade-off can be observed between patches being inside the CSZ for a long time and their reduced connectivity with the existing patches in the centre and southern part of the CSZ. This trade-off is particularly strong for small budgets (see Appendix D) and leads to the negative influence of the *climate migration effect* on cost-effectiveness.

The conceptual nature of our model limits the possibility of deriving direct policy implications of our results. Nevertheless, our model improves the general understanding of the influence of climate change on the cost-effective choice of governance modes and patch selection strategies for biodiversity conservation. We show that the cost-effectiveness of governance modes and patch selection strategies may be influenced by changing climatic conditions and thus policy makers are advised to explicitly include climate change concerns in their designs. The consideration of respective patch selection strategies to allow for specific targeting of species or climatic conditions is important in this context. In contrast, the patch selection strategy ‘price prioritisation’ shows no particular advantage with respect to changing climatic conditions, but allows for a potential standard alternative by generating easy to select, low cost conservation networks, albeit with low connectivity.

Generally, the more flexible or rigid character of conservation networks due to different governance modes and the resulting implications on cost-effectiveness should be accounted for in any decision about the optimal governance mode choice under climate change. These findings are in line with general calls for more adaptive management to deal with the impact of climate change on biodiversity (Cinner et al. 2018) and in particular with an increasing emphasis on adaptive and flexible management strategies in reserve site-selection problems—for example in the areas of dynamic fisheries closures (Dwyer et al. 2019), dynamic field flooding for water birds (Reynolds et al. 2017), and risk-dependent adaptive strategies for protected areas (Jacobs et al. 2019).

The aim of the research presented here was to understand how climate change parameters influence the relative cost-effectiveness of the two governance modes. Therefore, we did not focus on how changes in the ecological and economic parameters of our model impact the relative cost-effectiveness of the two governance modes and only present the results in Appendix D. In principle, these results are in line with those of Schöttker et al. (2016) who analysed changes in the ecological and economic parameters (e.g. available budget, interest rates, emigration and immigration characteristics of species) on the relative cost-effectiveness of the two governance modes, albeit without considering climate change. In particular, our findings confirm that increases in interest rates and budget lead to an increase in the overall cost-effectiveness of all governance mode options (for details see Figs. A7 and A8 in Appendix D). While Schöttker et al. (2016) find that the cost-effectiveness increase is stronger for land purchase than for landowner compensation, our study provides inconclusive evidence in that direction. Instead, it suggests that the choice of the specific patch selection strategy has to be considered as an additional factor (an aspect not covered by Schöttker et al. 2016). However, due to this aspect and the differences in

landscape layout in both studies (large, per-se suitable landscape in Schöttker et al. vs. small, changing CSZ in our study), the effects of the economic and ecological parameters are difficult to compare directly.

In designing the ecological-economic model, we made several simplifying assumptions that deserve discussion. Regarding conservation costs, we assumed that they are constant over the entire timeframe and unaffected by the agency's behaviour. By assuming constant costs we ignore any kind of strategic behaviour, for example from landowners overstating conservation costs to achieve higher payments or a higher price if they intend to sell their land (Banerjee et al. 2016; Gerling and Wätzold 2021; Kuhfuss et al. 2016). A strategic overstatement of conservation costs could increase patch prices in both governance modes, in turn reducing their cost-effectiveness. Further research is necessary to understand which governance mode is more prone to strategic behaviour and how to design possible mechanisms to reduce it. Furthermore, our assumption about constant conservation costs disregards that changing climatic conditions may lead to changes in the productivity of land and thus changing conservation costs and land prices (Gerling et al. 2021). We consider it an interesting and relevant avenue for further research to systematically investigate how the interplay of climate-driven changes in conservation costs and conservation performance of patches impacts on the cost-effectiveness of different governance modes and patch selection strategies (see Gerling et al. (2021) for a case study on this aspect).

Regarding the ecological side, we assumed that the conservation agency is interested in the protection of a single species, while a multi-species perspective is often applied in real world conservation programmes. Given that by combining economic, ecological and climate-related variables our model is already very complex, the decision to focus on one species was made for reasons of simplification. While it is rather straightforward to technically adapt the ecological-economic model to simulate more than one species at a time, understanding the reasons for the cost-effectiveness performance of different governance mode—patch selection strategy combinations against changes in climate parameters for different combinations of multiple species is beyond the scope of this paper. However, based on the results of the sensitivity analysis of ecological parameters (Appendix D) it can be seen that survival probabilities in a given governance mode- patch selection strategy scenario and under given climatic conditions depend on species characteristics. It is thus plausible that in a multi-species protection situation, a mix of different governance modes and patch selection strategies might be a suitable option to cater for the needs of different target species at the same time (Drechsler et al. 2016). Further research is however necessary in this direction.

With respect to the governance structure, we only considered two governance modes that are polar types of governance structure and ignored hybrid governance modes. For example, a conservation agency might split its budget and spend part of it to buy areas and the rest on compensation contracts with landowners. By doing so, benefits of both governance modes might be combined (e.g. fixed location of purchased patches with ecologically beneficial effects, and adaptability of compensated areas with changing climatic conditions). However, an analysis of the extent to which benefits are combined and what other effects may occur is a matter of further research.

In our model we further assumed that the conservation agency is allowed to sell patches in the *buy alternative*, as patches that are no longer in the CSZ for a specific species no longer provide a suitable habitat for that species (cf. Alagador et al. 2014). Thus, the budget regained from selling these patches can be utilised to purchase new patches at more suitable locations. The assumption of land sale possibilities can be seen as the foundation of the conservation agency's flexibility, necessary to adapt conservation site

selection to the changing climatic conditions in the landscape. It has to be mentioned, however, that it may not be possible in reality for a conservation agency to sell conserved land due to legal restrictions regarding the permanence of conservation areas (Schöttker and Wätzold 2018) and because the land may be used for the conservation of other species. As a result, agencies would be unable to react swiftly to changing ecological and climatic conditions in the landscape, thereby reducing the cost-effectiveness of the *buy alternative* in comparison to the *compensation alternative*.

Similarly, we assumed that land can always be purchased by a conservation agency and landowners are always willing to carry out conservation measures on their land once the compensation payment exceeds the opportunity costs of conservation. However, in reality landowners may not be willing to sell their land (Knight et al. 2011; Selinske et al. 2015) or carry out conservation measures on it even if it is profitable to them (Schenk et al. 2007). In this context, Schöttker et al. (2016) already showed a negative impact on the cost-effectiveness of the compensation alternative in comparison to the buy alternative due to a decreasing willingness among landowners to carry out conservation measures. We leave it to further research to investigate in more depth how different assumptions about land availability influence the cost-effectiveness of the different governance modes and patch selection strategies and how different strategies on the part of the conservation agency perform in this context (for example, by buying land which is not yet inside the CSZ, but will be in the near future).

Alternatively, instead of looking at the dichotomy of land purchase versus landowner compensation, which is rooted in Williamson's analysis of the firm (Williamson 1998, 1989), one can also investigate more broadly how different policy options perform under climate change in terms of cost-effectiveness and compare them with the options of land purchase and landowner compensation (Gerling and Wätzold 2021). This may include options such as leasing land (Juutinen et al. 2008), conservation easements (Schöttker and Santos 2019), offsetting schemes (Gerling and Wätzold 2021) and result-oriented payments (Burton and Schwarz 2013) as an alternative form of compensation payments.

More generally, one may also investigate the spatial level on which decisions about conservation measures under climate change should be made. This may be an interesting question with respect to differences in information availability (e.g. one may assume that species-specific information is more available locally whereas information on climate change is better accessible on a more centralised level). It may also be an interesting question with respect to the perspective of the decision maker. Decisions on a centralised level may take into account the fact that a species is in the landscape under consideration for a very long time, whereas localised decisions may consider that a species is only in the local landscape for a comparatively short period due to a decreasing climate suitability. Such analyses may profit from insights from debates about environmental federalism, where related aspects have been discussed (e.g. Oates 2001). We leave it to further research to address the topic of the appropriate spatial level of decisions.

While we applied a conceptual ecological-economic model for our investigation, further research may also investigate the topic of this work with more empirical data in real landscapes. Climate models are able to provide precise estimations about future climate developments on a regional level; species-specific ecological models are able to assess the impacts of conservation measures in a changing climate, and the development of scenarios about future costs is feasible. Such models and data may be combined in empirical climate-ecological-economic models (compare Drechsler et al. 2021 and Gerling et al. 2021 for such model types) providing policy makers with important recommendations about

cost-effective governance mode and patch selection strategy choices. We hope our model motivates such future work and provides a useful basis for it.

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