Climate change, species range shifts and dispersal corridors: an evaluation of spatial conservation models

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Summary

1. The notion that conservation areas are static geographical units for biodiversity conservation should be revised when planning for climate-change adaptation. Since species are expected to respond to climate change by shifting their distributions, conservation areas can lose the very same species that justified their designation. Methods exist to take into account the potential effects of climate on spatial priorities for conservation. One of such methods involves the identification of time-ordered linkages between conservation areas (hereafter termed climate-change corridors), thus enabling species tracking their suitable changing climates.

2. We critically review and synthesise existing quantitative approaches for spatial conservation planning under climate change. We extend these approaches focusing on the identification of climate-change corridors, using three alternative models that vary on the objective function (minimum cost or maximum benefit sought) and on the nature of conservation targets (area-based or persistence probabilities).

3. The three models for establishing climate-change corridors are illustrated with a case study involving two species distributed across the Iberian Peninsula. The species were modelled in relation to climate-change scenarios using ensembles of bioclimatic models and theoretical dispersal kernels. The corridors obtained are compared for their location, the temporal sequence of priorities, and the effectiveness with which solutions attain persistence and cost objectives.

4. By clearly framing the climate-change corridors problem as three alternative models and providing the corresponding mathematical descriptions and solving tools, we offer planners a wide spectrum of models that can be easily adapted to a variety of conservation goals and constraints.

Key-words: connectivity, conservation planning, effectiveness, efficiency, graph theory, *Marxan*, mathematical programming, network flow, persistence, prioritisation, reserve selection, *Worldmap*, *Zonation*

Introduction

Climate change poses major challenges to conservation planning because species distributions are affected in complex and seemingly idiosyncratic ways (Thomas *et al.* 2004; Hof *et al.* 2011; Garcia *et al.* 2014). Responses of species to climate change might include range contractions and expansions, local adaptation with range stasis or full displacement of ranges with range size remaining constant. With such a variety of responses, static conservation areas are unlikely to meet the needs of multiple species under climate change (Araújo *et al.* 2004, 2011; Hannah *et al.* 2007; Kujala *et al.* 2011). There are a number of approaches for spatial conservation planning that deal with such challenges (*sensu*, Araújo 2009). Some seek the identification of conservation areas predicted to remain climat-

ically stable through time (i.e. climatic refugia, Keppel *et al.* 2012). Others pursue the identification of areas for expansion of already established conservation areas (Hodgson *et al.* 2011), the design of functional networks of protected areas to safeguard processes running at a regional scale (Hannah *et al.* 2007; Hole *et al.* 2009), the identification of climate-gradient corridors (Nuñez *et al.* 2013) or land-facet corridors (Brost & Beier 2011), and importantly, the preservation of areas where species range adaptation to climate change is more likely (Nuñez *et al.* 2013; Hannah *et al.* 2014).

Several studies have been developed to address the challenges of spatial conservation planning under climate change (for a review, see Table 1). These studies typically use off-the-shelf conservation planning software such as *Marxan* (Ball, Possingham & Watts 2009) or *Zonation* (Moilanen, Kujala & Leathwick 2009) (see Appendix S1). These softwares use optimisation algorithms developed to solve minimum cost (hereafter min-cost) and maximum representation (hereafter max-

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Table 1. Summary table of studies using spatial conservation prioritisation tools to deliver solutions in a context of climate change, departing from bioclimatic niche model outputs. These studies are classified in terms of the specific methodological variations used within each software tool (Tool component), the type of algorithm and a relative measure of time needed for solving (Algorithm), the availability of the quantitative tool (Availability), a brief description of main data (Biodiversity and climate data), the methodological details that enable the software to replicate a climate-change problem (Methodological singularity), how dispersal data are integrated (Dispersal data), the final spatial planning output from the study (Mapping) and the corresponding study references (Refs)

Tool component	Algorithm	Availability	Biodiversity and climate data	Methodological singularity	Dispersal data	Mapping	Refs
Marxan (13 studies)							
Basic	Heuristic. Fast processing times	Stand-alone freeware software	Time-based presence/absence or local suitability based on climatic conditions	Use of biodiversity data as features. Analysis for each time period	No data or dispersal constraints implemented in bioclimatic niche modelling	A map optimising predictions in each time period	Shaw et al. (2012)
				Use of biodiversity data as features. Analysis for each time period. Fixing solution from the previous time period	No data		Rayfield et al. (2008)
			Presence/absence data and a local climate stress data	Use of biodiversity data as features. Local climatic conditions as a cost layer			Allnutt et al. (2012)
				Use of biodiversity data and local conditions as features			Levy & Ban (2013)
			Classes of suitability change from a baseline to a future time period (per species)	Use of classes of change as features	No data	A map optimising predictions in each time period followed by a map optimising predictions for each change scenario	Amorim et al. (2014)
Fixed budget and penalties for unmet targets	Heuristic. Fast processing times		Local suitability based on climatic conditions	Use of biodiversity data as features	Non-dispersal scenario in bioclimatic niche modelling	A map optimising predictions in each time period followed by a map matching solutions obtained for two time periods	Carvalho et al. (2011)
				Use of biodiversity data as features. Analysis for each time period. Fixing solution from the previous time period	No data	A map optimising predictions in each time period	Loyola et al. (2013)
			Local suitability and a local climate stress data	Use of biodiversity data as features. Local climatic conditions as a cost layer		A map optimising predictions in each time period	Game et al. (2008, 2011); Klein et al. (2013)

Table 1. (continued)

Tool component	Algorithm	Availability	Biodiversity and climate data	Methodological singularity	Dispersal data	Mapping	Refs
Boundary layer penalty	Heuristic. Fast processing times		Presence/absence data and a local climate stress data	Use of biodiversity data as features. Local climatic conditions to identify climatic refugia, using boundary penalties	Implicit in promoting contiguous solutions	A map optimising predictions in each time period	Hermoso, Ward & Kennard (2012, 2013)
						A map integrating several time periods (linked by a general boundary rule)	Makino *et al.* (2014)
Zonation (11 studies)							
Basic and smoothed	Heuristic. Fast processing times	Stand-alone freeware software	Time-based presence/absence, local suitability or abundance data based on climatic conditions	Use of biodiversity data for each time period (weighting possible)	Species-specific kernel (for smoothed applications)	A map optimising predictions in each time period	Klorvuttimontara, McClean & Hill (2011); Runting, Wilson & Rhodes (2013); Summers *et al.* (2012); Leach, Zalat & Gilbert (2013); Williams *et al.* (2013); Wan *et al.* (2014)
				Use of biodiversity data for all time periods (weighting possible)	No data	A map integrating several time periods	Bond, Thomson & Reich (2014)
			Presence/absence data and a local climate stress data	Use of biodiversity data and local climatic conditions as features (weighting possible)	No data	A map integrating several time periods	Allnutt *et al.* (2012)
Species interaction	Heuristic. Medium-to-fast processing times		Local suitability based on climatic conditions	Use of biodiversity data for all time periods plus species-specific interaction layers (weighting possible). Possibility to use local predictive uncertainty as cost data	Species-specific kernel	A map integrating several time periods and interaction layers	Carroll, Dunk & Moilanen (2010); Faleiro, Machado & Loyola (2013); Kujala *et al.* (2013); Lemes & Loyola (2013)
Corridor-based approaches (3 studies)							
Worldmap	Heuristic. Medium-to-fast processing times	Stand-alone private software	Time-based presence/absence, based on climatic conditions	Use of biodiversity data as features	Species-specific kernel	A map integrating data from previous time periods	Williams *et al.* (2005)
Network flow	Optimal. Slow processing times	Several solvers (commercial, academic and free online)	Time-based presence/absence, based on climatic conditions	Use of biodiversity data as features	Species-specific kernel	A map integrating data from previous time periods. A map for each time period (optimising data for all the time horizon)	Phillips *et al.* (2008) Alagador, Cerdeira & Araújo (2014)

representation) problems (Pressey *et al.* 1993; Pressey, Possingham & Margules 1996; Billionnet 2013), with modifications to address a wide range of specific problems in conservation planning such as ones driven by climate-change impacts (e.g. Lehtomäki & Moilanen 2013).

When implemented to address spatial conservation planning problems under climate change, existing software tends to neglect a number of important issues. First, solutions obtained with *Marxan* and *Zonation* are commonly obtained with optimisation running with data layers summarising expected trends of biological features in a given time interval, or using several time periods with biological data pooled together (for a review and some examples on the issue, see Tables 1 and S1). These solutions do highlight priority areas, but give no information on the time period each area gains relevancy to be selected (i.e. scheduling plans for the selected areas).

Secondly, and related with the previous point, the solutions obtained from general-purpose software do not define time-aligned planning units that, apart from scheduling, would also enable planners to assess the effect that a given area selected in a given time period has on the conservation value of the same or other areas in other time periods. Information such as this would allow planners to assess the impact that habitat degradation within an area imposes, and at what level the habitat in another area within the same planning unit should be recovered in order to compensate species persistence from such habitat degradation. Analyses such as these may be applied to drive offset evaluations.

Thirdly, although existing software can take into account changes in the distributions of species, they do not account for changes in conservation area costs. This gap limits conservation planning in attending the most cost-effective estimates to conserve biodiversity in time (Balmford *et al.* 2003).

Overcoming these limitations requires approaches specifically designed to enable prioritisation of areas through time. Williams *et al.* (2005) pioneered the development of dynamic approaches for spatial conservation prioritisation by proposing a new heuristic method to identify conservation areas that define time-based dispersal corridors (herein named climate-change corridors), required for the conservation of species under climate-change scenarios. Later, Phillips *et al.* (2008) translated the climate-change corridor identification problem into a mathematically formalised network flow problem that, coupled with optimisation methods, provided planners with more efficient solutions. With this approach, Phillips *et al.* (2008) were able to reduce by a third the area required to meet the conservation targets established by Williams *et al.* (2005). Williams *et al.* (2005) and Phillips *et al.* (2008) addressed the problem of identifying a given number of independent climate-change corridors, that is time-ordered sequences of areas, for each species using a minimum number of areas. Within both assessments, the set of climate-change corridors defined for a given species entails an independence requirement, such that no two corridors identified for a species may pass over the same area in the same time period. Alagador, Cerdeira & Araújo (2014) extended the framework of Williams *et al.* (2005) and, also using a predetermined minimum number of corridors

to be selected per species, proposed to maximise the combined persistence of the set of species subjected to a fixed budget available to invest on area conservation. This model also accommodates the possibility of planners replacing the areas that, although selected in a given time period, are expected to become ineffective in the future by new areas becoming suitable for the species.

Here, we expand on previous developments and use mathematical programming to give a unified framework for modelling distinct approaches addressing spatial conservation planning under climate change based on the concept of climate-change corridors, as introduced by Williams *et al.* (2005) and Phillips *et al.* (2008) and later extended by Alagador, Cerdeira & Araújo (2014). We introduced novel variants that rely on a quantified notion of species persistence along climate-change corridors and discuss the pros and the cons of the different models. A small case study is used to illustrate and compare the different proposals. It can be concluded that solutions obtained from different models may differ significantly in the areas identified as priorities along time and in the corresponding species persistence expectancies.

Materials and methods

Mathematical programming formulations for optimal selection of climate-change corridors for three realistic conservation problems are provided. First, we formalise the minimum-cost problem developed by Williams *et al.*(2005) and refined by Phillips *et al.*(2008) (hereafter *MinCost*). Secondly, we present the maximum representation formulation introduced by Alagador, Cerdeira & Araújo (2014) (hereafter *MaxPersistNetFlow*) together with a reformulation of that same problem, that makes mathematically explicit climate-change corridors as independent selection units (*MaxPersistCorridor*). Thirdly, based on this same formulation of corridors as explicitly stated selection units, we define a novel min-cost model, similar to *MinCost* but using persistence metrics as targets for each of the species (*MinCostPersist*) (Fig. 1). We finalise discussing adjustments to these models that could be additionally implemented to increase realism of conservation planning solutions (e.g. consideration of dynamic costs, dynamic selection of areas, and generation of sets of several 'good-quality' solutions).
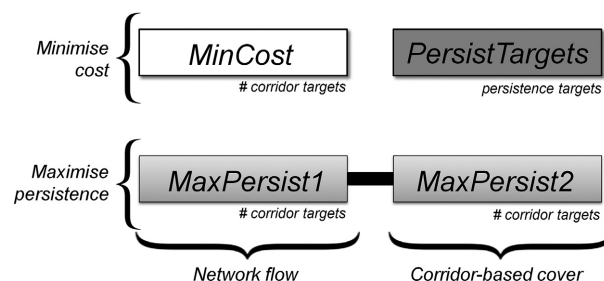

Fig. 1. Conceptual variations of the climate-change conservation problem. *MinCost*: min-cost model using species presence/absence data. The remaining problems use suitability data: *MaxPersistNetFlow* and *MaxPersistCorridor* define a maximum-persistence model with areal representation (i.e. number of corridors) targets, formulated as a network flow (*MaxPersistNetFlow*) and as a corridor-based selection problem (*MaxPersistCorridor*), and *MinCostPersist* defines a minimum-cost model with species persistence targets. Like *MaxPersistCorridor*, it is formulated as a corridor-based selection problem.

Table 2. Notation used in problem formulations

Parameters

S	Set of species
I	Set of planning units in the study area
T	Time periods in analysis $\{1,2,\ldots,t_z\}$
I_s^t	Set of planning units considered to be suitable for species s to occur at time t
sr	The source node of a species network flow formulation
cor_s	Set of corridors for species s
$cor_s^{i,t}$	Set of corridors for species s with planning unit i defined for time t
Tg_s	Number of corridors to be selected for species s
P_s	The minimum persistence to be achieved for species s
B	Total budget for allocating planning units for conservation
$po_s^{i,t}$	Probability of occurrence of species s in planning unit i in time t given local environment
$pd_s^{i,j,t}$	Probability of species s to colonise successfully planning unit j in time $t+1$ from i in time t
pt_s^l	Probability of species s to persist in corridor l
c_i	Cost of acting on planning unit i
c_i^t	Cost of acting on planning unit i in time t
$\hat{c}_i^t$	Profit from releasing planning unit i in time t
Control variables	
x_i	Variable indicating if planning unit i is selected (1) or not (0)
x_i^t	Variable indicating if planning unit i is selected (1) or not (0) in time t
$x_i^{t,t+1}$	Variable indicating if planning unit i was selected in time t and deselected in time $t+1$ (1) or not (0)
$f_s^{sr,i}$	Variable indicating the amount of flow on arc i of type 1 for species s
$f_s^{i,t}$	Variable indicating the amount of flow on arc (i,i) of type 2 of period t, for species s
$f_s^{i,j,t}$	Variable indicating the amount of flow on arc (i,j) of type 3 from period $t–1$ to period t, for species s
z_s^l	Variable indicating that corridor l is selected (1) or not (0) for species s
r_i^t	Variable indicating that planning unit i was released in time t
X	A set of pairs (i,t) indicating the planning units, i, and time periods, t, that were targeted in the previous model run $(x_i^t = 1)$

To describe the alternative conceptualisations of the climate-change corridors problem, we use the following notation (see Table 2 for a summary of parameters and variables). We call $T = \{1,2,\ldots,t_z\}$ the set of t_z time periods to be considered, I the set of planning units in the geographic region where the conservation prioritisation study takes place, and S the set of species to be conserved. We use I_s^t to denote the set of planning units in I where climate is considered suitable for species $s \in S$ in time period t. We also assume that, for every planning unit i, there is a cost c_i for using it for conservation purposes. In conservation planning, costs typically define the amount of financial investment needed to conserve biodiversity (e.g. implementation, management, land acquisition and opportunity costs), but when information on conservation costs is unavailable, surrogates for cost are often used (e.g. proportion of area already committed to conservation).

MINIMUM-COST DISPERSAL CORRIDORS (*MINCOST*)

Phillips *et al.* (2008) used network flows (see Ahuja, Magnanti & Orlin 1993 for an introduction to the theme) to formulate the climate-change conservation planning problem introduced by Williams *et al.* (2005).
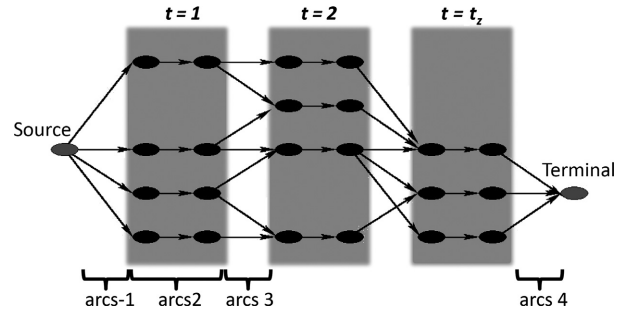

Fig. 2. Schematic representation of a network defining the spatial distribution of a species along time in a given geographic region. Adapted from Phillips *et al.* (2008).

For each species $s \in S$, a network is defined as follows (see Fig. 2). In each time period, $t \in T$, two twin-node sets are constructed, $I_{1,s}^t$, $I_{2,s}^t$, representing two copies of each planning unit, $i \in I_s^t$. A source node, sr, and a terminal node, sk, are also defined. The replicates of planning units and the source and terminal nodes are added for operational purposes as will become clear further down. In each of these networks, four types of arcs exist as follows: (i) arcs linking the source node sr to every node in $I_{1,s}^1$; (ii) arcs linking each node in $I_{1,s}^t$ with the corresponding twin in $I_{2,s}^t$; (iii) arcs linking nodes in $I_{2,s}^t$ to nodes in $I_{1,s}^{t+1}$ if individuals from the species can move directly between the corresponding areas in the time interval $[t,t+1]$; and (iv) arcs linking every node of $I_{2,s}^{t_z}$ with the terminal node sk. To every arc (i,i) of type 2, it is assigned the cost c_i associated with the planning unit i. To every other arc in the network, a cost equal to zero is assigned.

Given a number of corridors, Tg_s, to be identified for each species s, the formulation of Phillips *et al.* (2008) of the minimum-cost climate-change corridor problem (*MinCost*) is as follows (see Table 2 for a summary of parameters and variables):

$$\min \sum_{i \in I} c_i x_i \qquad \text{eqn 1}$$

$$\sum_{i \in I_{1,s}^1} f_s^{sr,i} = Tg_s \quad \forall s \in S \qquad \text{eqn 2}$$

$$f_s^{i,t} \leq x_i \quad \forall s \in S, \forall i \in I_s^t, \forall t \in T \qquad \text{eqn 3}$$

$$f_s^{sr,i} = f_s^{i,1} \quad \forall s \in S, \forall i \in I_{1,s}^1 \qquad \text{eqn 4}$$

$$f_s^{i,t} = \sum_{j \in I_{1,s}^{t+1}} f_s^{i,j,t+1} \quad \forall s \in S, \forall i \in I_s^t, \forall t \in T \setminus \{t_Z\} \qquad \text{eqn 5}$$

$$\sum_{j \in I_{2,s}^t} f_s^{j,i,t} = f_s^{i,t} \quad \forall s \in S, \forall i \in I_s^t, \forall t \in T \setminus \{1\} \qquad \text{eqn 6}$$

$$f_s^{i,t} \in [0,1] \quad \forall s \in S, \forall i \in I_s^t, \forall t \in T \qquad \text{eqn 7}$$

$$f_s^{i,j,t} \in [0,1] \quad \forall s \in S, \forall (i,j) : i \in I_{2,s}^t \wedge j \in I_{1,s}^t, \forall t \in T \setminus \{1\} \qquad \text{eqn 8}$$

$$f_s^{sr,i}, f_s^{j,sk} \in [0,1] \quad \forall s \in S, \forall i \in I_{1,s}^1, \forall j \in I_{2,s}^{t_z} \qquad \text{eqn 9}$$

$$x_i \in \{0,1\} \quad \forall i \in I \qquad \text{eqn 10}$$

In this formulation, x_i are zero–one variables that indicate whether the planning unit i is selected ($x_i = 1$) or not selected ($x_i = 0$) for conservation; $f_s^{i,t}$ are flow variables specifying the amount of flow on arcs linking the twin nodes (i,i) in the same time period t (arcs of type 2); $f_s^{i,j,t}$ are flow variables that indicate the amount of flow that passes on arcs

linking planning unit i in time t–1 with planning unit j in time t (arcs of type 3); and $f_s^{sr,i}$ and $f_s^{i,sk}$ indicate the passage of flow along arcs of type 1 and type 4, respectively. The objective function (Eqn 1) minimises the sum of costs (c_i). Equations 4–6 define the flow conservation constraints for each interior node (i.e. every node except source sr and terminal sk) stating that the flow entering each node equals the flow leaving the node. These constraints ensure connectivity of corridors in different periods of time (i.e. corridors correspond to paths from node sr to node sk). Equation 2 defines the number of corridors for each species s to be Tg_s, the established targets for species s. Inequalities in Eqn 3 relate the flow variables with the decision variable x_i. They force x_i to be positive ($x_i = 1$), whenever the amount of flow on any arc (i,i) of type 2 is positive. Equations 7–10 define the range of variables.

Importantly, given the mathematical structure of the problem, variables x_i may be defined as continuous in the interval [0,1]. This takes advantage of the integrality theorem that states that, as long as all the problem-defining parameters (i.e. the flow required for each species, and the capacity of the arcs of the network) are integers, there is an optimal solution to the continuous linear programme consisting of only integer flows (Ahuja, Magnanti & Orlin 1993). This theorem is of high convenience given that the integer problem can be efficiently solved as a standard minimum-cost network flow problem. In the end, and although not constrained to it, the flow that enters each node and the variables x_i will be zero or one, thus clearly identifying the Tg_s climate-change corridors identified for each species s and the selected areas, respectively.

MAXIMUM-PERSISTENCE CORRIDORS (*MAXPERSISTNETFLOW*)

In the previous *MinCost* model, corridors include areas where species are predicted to occur after a threshold is applied to convert continuous projections of climate suitability for species into projections of species presence or absence. Dispersal of species between two areas is also assumed to be binary (i.e. it either occurs or does not occur). These binary representations of continuous processes are simplifications of complex biological patterns and processes that are more meaningfully handled using a probabilistic framework (Araújo & Williams 2000; Williams & Araújo 2002). To overcome these limitations, Alagador, Cerdeira & Araújo (2014) proposed to adjust the *MinCost* framework with the following: (i) continuous projections of climate suitability for species, which, under specific circumstances of data collection (randomised presence–absence records across the study region), can be assimilated to probabilities of species occurrence (Peterson *et al.* 2011) so that $po_s^{j,t}$ is the probability of species s to occur at planning unit j, in time period t; and (ii) a dispersal model describing the probability of a species to successfully move from one area to another in a given time interval. Parameters $pd_s^{i,j,t}$ define the probability for species s to move from area i to j during the time interval between periods t–1 and t. With these data, a persistence-like index is developed, so that the probability (pt_s^l) of a species, s, to persist in corridor, $l = (i,j,..,k,m)$, across $1,2...,t_z$ time periods may be quantified as follows:

$$pt_s^l = po_s^{i,1} \times pd_s^{i,j,1} \times po_s^{j,2} \times \ldots \times pd_s^{k,m,t_z-1} \times po_s^{m,t_z} \qquad \text{eqn 11}$$

The model proposed by Alagador, Cerdeira & Araújo (2014), here referred as *MaxPersistNetFlow*, is obtained from *MinCost* replacing the objective function Eqn 1 by

$$\max \prod_{s \in S} \prod_{i \in I_s^t} \prod_{j \in I_{1,s}^t} \left[\prod_{t \in T} (po_s^{i,t} f_s^{i,t}) \prod_{t \in T \setminus \{t_z\}} (pd_s^{i,j,t} f_s^{i,j,t}) \right] \qquad \text{eqn 12}$$

which, linearised, becomes

$$\min - \sum_{s \in S} \sum_{i \in I_s^t} \sum_{j \in I_{1,s}^t} \left[\sum_{t \in T} \log(po_s^{i,t}) f_s^{i,t} + \sum_{t \in T \setminus \{t_Z\}} \log(pd_s^{i,j,t}) f_s^{i,j,t} \right] \qquad \text{eqn 13}$$

and adding the budget constraint

$$\sum_{i \in I} \sum_{t \in T} c_i x_i \leq B \qquad \text{eqn 14}$$

The objective function (Eqn 12, loglinearised in Eqn 13) combines the persistence probabilities defined in Eqn 11 for all the species across all the corridors. It translates as the probability of all the species to persist along time within all their selected corridors. Constraint in Eqn 14 defines the maximum allowed solution cost (i.e. the budget available across all time horizon, if cost stands for an economic factor). Importantly, Eqn 10 cannot be relaxed as in the previous model, thus making *MaxPersistNetFlow* harder to solve than *MinCost*.

By increasing the budget, values of the objective function Eqn 12 increase until a plateau is reached, after which budgets are no longer constrains and the optimal solutions may be obtained taking the problem for each species independently (i.e. the Tg_s non-overlapping corridors that for each species s maximise the product of persistence). In other words, persistence of species in such solutions becomes limited by the rate of climate change and species dispersal abilities alone. The solutions obtained for large budgets essentially reproduce the case where species are able to colonise the best suitable areas as if they quickly reached equilibrium with climate (Araújo & Pearson 2005; García-Valdés *et al.* 2013). For smaller budgets, trade-offs among species occur and less suitable and/or more distant (but less costly) planning units might be selected.

ADDRESSING AREA RELEASE

The *MinCost* and *MaxPersistNetFlow* models generate solutions in which a planning unit is selected because it adds value to the conservation areas at a given moment in time but not necessarily throughout the entire period of the conservation plan. Modifications of these models enable planners to optimally schedule conservation decisions with full control of the timing to allocate financial resources into conservation (see Alagador, Cerdeira & Araújo 2014).

Scheduling of conservation decisions is based on the premise that areas that lose value with time can be replaced by better performing areas. Obviously, there is a wide array of conservation values that might be rigid and might be invoked to justify the maintenance of specific conservation areas even when they are no longer effective in meeting specific conservation targets (for an example see Hiley *et al.* 2013). Release of conservation areas (also referred to as 'degazetting') should be made with caution, especially when the area release is driven by model predictions with great variability or uncertainty (Fuller *et al.* 2010).

To implement the dynamic process of selection and release of conservation areas, the variables related with area selection, x_i, and their varying costs, c_i, should be decomposed into x_i^t and c_i^t, respectively, specifying the time period t under consideration.

To adjust model *MinCost* to handle area release, the objective function (Eqn 1) is replaced by

$$\min \sum_{i \in I} \sum_{t \in T} c_i^t x_i^t \qquad\qquad \text{eqn 15}$$

and constraints Eqn 3 by

$$f_s^{i,t} \leq x_i^t \quad \forall s \in S, \forall i \in I_{1,s}^t, \forall t \in T \qquad \text{eqn 16}$$

Constraints Eqn 10 turn to

$$x_i^t \in \{0,1\} \quad \forall i \in I, \forall t \in T \qquad\qquad \text{eqn 17}$$

To adjust *MaxPersistNetFlow*, besides using Eqns 16 and 17 to replace Eqns 3 and 10, respectively, Eqn 14 is replaced by

$$\sum_{i \in I} \sum_{t \in T} c_i^t x_i^t \leq B \qquad\qquad \text{eqn 18}$$

MAXIMUM-PERSISTENCE CORRIDORS, USING CORRIDORS AS SELECTION UNITS (*MAXPERSISTCORRIDOR*)

Because solutions to the *MaxPersistNetFlow* problem are much harder to obtain when compared with the minimum-cost flow problem *Min-Cost*, an alternative formulation using climate-change corridors as planning units clearly presents practical advantages. In the heuristic algorithm proposed by Williams *et al.* (2005), a pool of 1000 climate-change corridors is randomly selected for each species in order to restrict corridor selection to workable-sized sets of selection units. A similar implementation can be replicated for *MaxPersistNetFlow*. However, because corridors are qualified differently based on their persistence metrics, instead of selecting corridors randomly, a pool consisting of the top k corridors ranking higher for persistence is defined. The greater the number of candidate corridors, k, the greater will be the computational effort to obtain a conservation solution. A practical approach is to start with a manageable number of top-ranking climate-change corridors and increase this number during the selection process as needed for reaching species persistence targets and/or to reduce the cost of the overall solution below some predetermined value.

Once defined a pool of corridors for each species, cor_s, and a set of variables z_s^l to indicate whether corridor l, assigned to species s, is selected ($z_s^l = 1$) or not ($z_s^l = 0$), the problem can be formulated as follows:

$$\max \prod_{s \in S} \prod_{l \in cor_s} pt_s^l z_s^l \qquad\qquad \text{eqn 19}$$

which is linearised to

$$\min \left(-\sum_{s \in S} \sum_{l \in cor_s} \log(pt_s^l) z_s^l \right) \qquad \text{eqn 20}$$

and subjected to the constraints

$$\sum_{l \in cor_s} z_s^l \geq Tg_s \quad \forall s \in S \qquad\qquad \text{eqn 21}$$

$$\sum_{l \in cor_s^{i,t}} z_s^l \leq 1 \quad \forall i \in I_s^t, \forall t \in T, \forall s \in S \qquad \text{eqn 22}$$

$$x_i^t \leq \sum_{s \in S} \sum_{l \in cor_s^{i,t}} z_s^l \quad \forall i \in I_s^t, \forall t \in T, \forall s \in S \qquad \text{eqn 23}$$

$$x_i^t \geq z_s^l \quad \forall s \in S, \forall i \in I, \forall t \in T, \forall l \in cor_s^{i,t} \qquad \text{eqn 24}$$

$$z_s^l \in \{0,1\} \quad \forall s \in S, l \in cor_s \qquad\qquad \text{eqn 25}$$

and Eqns 17 and 18, where $cor_s^{i,t}$ stands for the subset of corridors cor_s that includes area i in time period t.

The objective function Eqn 19 retrieves the product of persistence scores among all the selected corridors, and therefore, needs to be log-linearised (Eqn 13). Constraints in Eqn 21 define the number of corridors being selected for each species. Constraints in Eqn 22 ensure that among each set of non-independent corridors only one can be selected. Constraints Eqns 23 and 24 relate variables associated with planning units with variables associated with corridors. Together they state that planning unit i will be selected for period t (i.e. $x_i^t = 1$) if, and only if, selected corridor includes planning unit i in period t. With these conditions, zero-cost planning units will not be readily targeted to take part of the solution. Finally, Eqn 25 defines the range of variables related with the full selection of corridors.

MINIMUM-COST CORRIDORS WITH PERSISTENCE TARGETS (*MINCOSTPERSIST*)

MinCost, *MaxPersistNetFlow* and *MaxPersistCorridor* problems embody a shortcoming that can affect, particularly, the most vulnerable species (i.e. small range and/or species with limited dispersal). Although these models require a predetermined number of independent corridors for each species, their objective functions (minimising the sum of the costs of the selected areas in *MinCost*, or maximising the product of the persistence scores for all species in *MaxPersistNetFlow* and *MaxPersistCorridor*) do not prevent the possibility that the number of corridors selected for every species is insufficient for their long-term persistence. For example, *MinCost* corridors are made without information on the local climate suitability for species with the consequence that species might be represented in areas that are unsuitable for them. For *MaxPersistNetFlow* and *MaxPersistCorridor*, implemented with restricted budgets, severe trade-offs are likely to emerge while maximising the objective function. Given that the most threatened species are likely to have the lowest persistence expectancies within corridors (because of weak climatic suitability and/or more constrained dispersal abilities), their contribution to the overall persistence metric is lower than that of species with greater persistence expectancies. Therefore, threatened species tend to weight less in the objective function when compared with the more persistent species. In order to tackle such expected biases, a minimum-cost climate-change corridor model can be designed with persistence targets being defined *a priori* for each of the species.

Like *MaxPersistCorridor*, model *MinCostPersist* also starts with a set of corridors, cor_s, for each species using the objective Eqn 15, subject to constraints Eqns 17, 22–25, and changing *MaxPersistCorridor*'s constraints Eqn 21 by

$$\sum_{l \in cor_s} pt_s^l z_s^l \geq P_s \quad \forall s \in S \qquad\qquad \text{eqn 26}$$

Here, instead of requiring a certain number of corridors for each species, that might not guarantee that the combined persistence targets are met, we explicitly impose lower bounds on the combined corridor persistence scores for each species (Eqn 26).

ADDITIONAL FEATURES

Economic incomes from area release

When budgets are limited (they usually are) and the biological systems are highly dynamic (they usually are), release of conservation areas from strict conservation regulation might be considered

(e.g. selling, renting, licensing) in order to release funds to be directed to other conservation areas. It is possible that, in period t when area i is released, a financial return, $\hat{C}_i^t$, is obtained that will be discounted from the total cost. To model this, we introduce a new set of decision variables, r_i^t, to indicate whether area i is released in period t (i.e. $x_i^{t-1} = 1 \wedge x_i^t = 0 \Rightarrow r_i^t = 1$) and if so, to carry over this local economic return to discount on the cost to conserve that same area in t. These variables are controlled through the following constraints:

$$r_i^t \leq x_i^{t-1} \quad \forall i \in I, \forall t \in T \setminus \{1\} \qquad \text{eqn 27}$$

$$r_i^t \leq 1 - x_i^t \quad \forall i \in I, \forall t \in T \setminus \{1\} \qquad \text{eqn 28}$$

$$r_i^t \in \mathcal{R} \quad \forall i \in I, \forall t \in T \setminus \{1\} \qquad \text{eqn 29}$$

The objective function Eqn 15 that holds for the min-cost problems (*MinCost* and *MinCostPersist*) turns to the following:

$$\min \sum_{i \in I} \left(\sum_{t \in T} c_i^t x_i^t - \sum_{t \in T \setminus \{1\}} \hat{c}_i^t \cdot r_i^t \right) \qquad \text{eqn 30}$$

and in max-persistence problems (*MaxPersistNetFlow* and *MaxPersistCorridor*), the budget constraint (Eqn 18) turns to

$$\sum_{i \in I} \left(\sum_{t \in T} c_i^t x_i^t - \sum_{t \in T \setminus \{1\}} \hat{c}_i^t \cdot r_i^t \right) \leq B \qquad \text{eqn 31}$$

Generating several solutions

There usually are more than one optimal solution for a given conservation problem. In some cases, it might be that planners are interested in comparing different solutions to explore for additional trade-offs that are not considered within the area selection formulation (e.g. socio-ecological and cultural values). A straightforward approach to produce m solutions is to sequentially solve the problem adding to the model, and at the end of iteration m, the constraint

$$\sum_{(i,t) \in X} x_i^t \leq |X| - 1 \qquad \text{eqn 32}$$

where X is the set of pairs (i,t) for which the solution obtained in the previous iteration defined $x_i^t = 1$, and $|X|$ represents the size of X. In practice, Eqn 32 turns the solution obtained in iteration m unfeasible for the problem to be solved in iteration $m + 1$.

COMPARING DISTINCT CONCEPTUAL APPROACHES – A CASE STUDY

In order to explore differences and similarities among *MinCost*, *MaxPersist* and *MinCostPersist* (integrating area release), we implement these models within a case study including two species: the European mink, *Mustela lutreola*, and the four-leaf clover, *Marsilea quadrifolia* across the Iberian Peninsula (see Appendix S2, for details on data). Analyses were undertaken using four time slices (a baseline period, 2020, 2050 and 2080) assuming the A1FI scenario of climate-change scenario (Nakicenovic *et al.* 2000). Planning unit costs were estimated based on the principle that areas already conserved are cheaper to manage than areas without conservation management, such that $c_i^t = 1 - PA/4$, where PA represents the fraction of the planning units covered with conservation areas (see Fig. S1) (see Alagador *et al.* 2012; and Araújo *et al.* 2011, for similar procedures).

In an ideal scenario, it would be possible to adequately mechanistically assess persistence of all species of conservation concern and use predictions to define conservation targets (e.g. Fordham *et al.* 2013b). However, because estimates of persistence are difficult to obtain for many species, area-based targets are standard practice. We started by solving *MaxPersistCorridor* using $Tg = 5$ and $Tg = 20$ for the European mink and the four-leaf clover, respectively. These targets are arbitrary and were settled for illustrative purposes. They define a small number of areas enabling one to investigate the reasons behind the differential performances arising from our proposed models. We then assessed the expected persistence score for each one of the two species within climate-change corridors (taken additively), and then used it as the persistence targets in the *MinCostPersist* problem. We also obtained a solution for the *MinCost* problem using the same number of corridors as for *MaxPersistCorridor*.

We ran these comparisons for a sequence of budgets for the *MaxPersistCorridor* problem (with a pool of 2500 corridors with the highest persistence scores for each of the species, see Fig. S2). Given that 25 corridors will be defined in total (in *MinCost* and *MaxPersistCorridor*), the most relaxed budget would be of 25 cost-units, assuming that all planning units had cost of 0·25 cost-units (i.e. $PA_i = 0$). We used the following budget set {13, 14, 16, 18, 20, 22 and 24 cost-units}. For budgets lower than 13 cost-units, solving *MaxPersistCorridor* became unfeasible, because for at least one of the species it was not possible to select the required number of corridors. For budgets higher than 24 cost-units, solutions remained fixed. For each budget, we counted the number of corridors (for *MinCostPersist*), the total cost, the combined and individual species persistence score achieved (taken additively and as a product), and the maximum, minimum and median persistence scores taken among the corridors defined for each species.

We used the mathematical programming solver IBM ILOG CPLEX 12.5 (IBM Research, New York, NY, USA) to solve these problems.

Results from the case study

Because *MinCost* problems do not include persistence constraints, such as the inclusion of rules for selection of highly suitable areas for species, and their goal is simply to minimise costs, they always retrieved less costly solutions than *MaxPersistCorridor* problem sets (Fig. 3a). In contrast, because *MinCostPersist* fixes targets disregarding the number of corridors included, meeting of suitability targets for budgets below 20 cost-units was obtained with fewer resources (i.e. less unprotected area). Differences between *MaxPersistCorridor* and *MinCostPersist* solutions got smaller as budget increased, but *MinCostPersist* always attained lower costs than equivalent *MaxPersistCorridor* solutions. For budgets higher than 22 cost-units, the optimal solutions obtained for *MaxPersistCorridor* and *MinCostPersist* did not differ regarding total cost, contrasting to the major differences among solutions when assessing them through persistence metrics either combined in the objective function or as species-specific targets.

Solutions using *MinCostPersist* always had the highest effectiveness in attaining species persistence additively for most of the budgets considered, although differences for *MaxPersistCorridor* solutions were negligible (Fig. 3b). Similarity between the two solutions results from the equivalence of *MaxPersistCorridor* and *MinCostPersist* when operated with large budgets, since for both problems selecting the highest
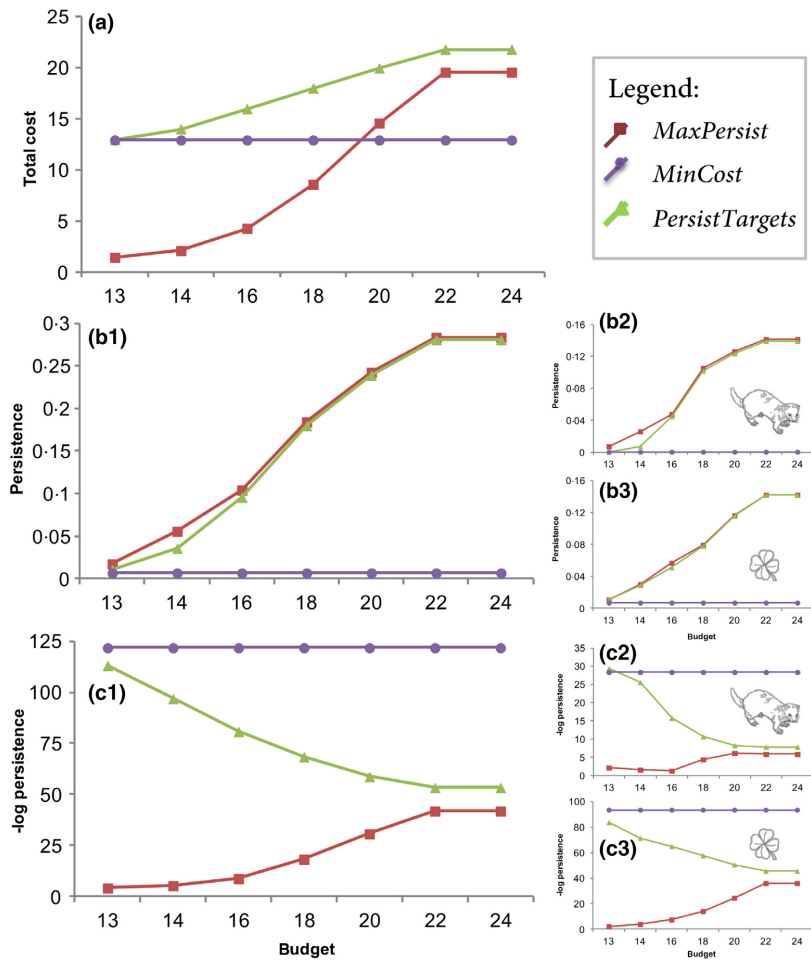
Fig. 3. Variation of solution performance with varying budgets using three conceptual models for identification of climate-change corridors for *Mustela lutreola* and *Marsilea quadrifolia* in Iberia Peninsula (projections made to 2080 with the A1FI climate-change scenario). (a) Total cost; (b1) additive persistence for the two species; (b2) additive persistence for *Mustela lutreola*; (b3) additive persistence for *Marsilea quadrifolia*; (c1) multiplicative persistence for the two species; (c2) multiplicative persistence for *Mustela lutreola*; and (c3) multiplicative persistence for *Marsilea quadrifolia*.

suitable and least costly planning units is the logical protocol to optimise their objective functions. However, when budgets are limited, the trade-offs characterising *MaxPersistCorridor* objective function (Eqns 12 and 13) decrease *MaxPersistCorridor*'s solution performance relative to *MinCostPersist*. This effect was particularly derived from the lower persistence expectancies of *Mustela lutreola* within its respective corridors (Fig. 3b2).

MaxPersistCorridor was the best-performing model for the highest budgets assessed, when the conservation value associated with the solutions is the product of persistence for the two species in their respecting corridors (i.e. probability of both species to be maintained across all the time horizon within all their respective identified corridors). In contrast, with increasing budgets, *MinCostPersist* displayed decreased effectiveness (Fig. 3c), as a result of the resulting increase in number of corridors to target (i.e. the higher the number of corridors, the less probable is the species to persist in all of them) (Table S2). However, across all budgets explored, *MinCostPersist* consistently attained best-performing solutions than *MaxPersistCorridor*s, because fewer corridors were required to achieve persistence targets.

When the conservation value of corridors is taken additively (i.e. the sum of persistence expectancies that, assuming statistical independence among corridors, equates to the expected number of species representations in the final time period), the performance of *MinCostPersist* obtained through budget variation was nonlinear, showing peaks for median persistence scores among corridors at mid-budgets. This is because the higher the budget the higher the persistence targets met and these were fulfilled with the selection of a great number of areas with both, low suitability scores and low cost, instead of resulting from high-quality area selections (because they do not exist or because their costs are too high) (see Figs 4 and S3).

The time required to obtain solutions for all of the 21 spatial conservation runs (7 budgets × 3 conceptual problems) varied between 0·5 s (*MinCost*) and 19 s (for *MaxPersistCorridor* with 21 cost-units constrained budget).

Discussion

We examined and described alternative mathematical formulations that enable planners to deal with climate-change effects in spatial conservation prioritisation frameworks. Taken together, the mathematical formulations provided herein offer the ability to solve different optimisation problems (minimum cost versus maximum benefit) and conservation challenges associated with species shifting climate suitabilities and dispersal needs. As shown in our case study, solutions can be highly distinct with performances varying with the specific framework
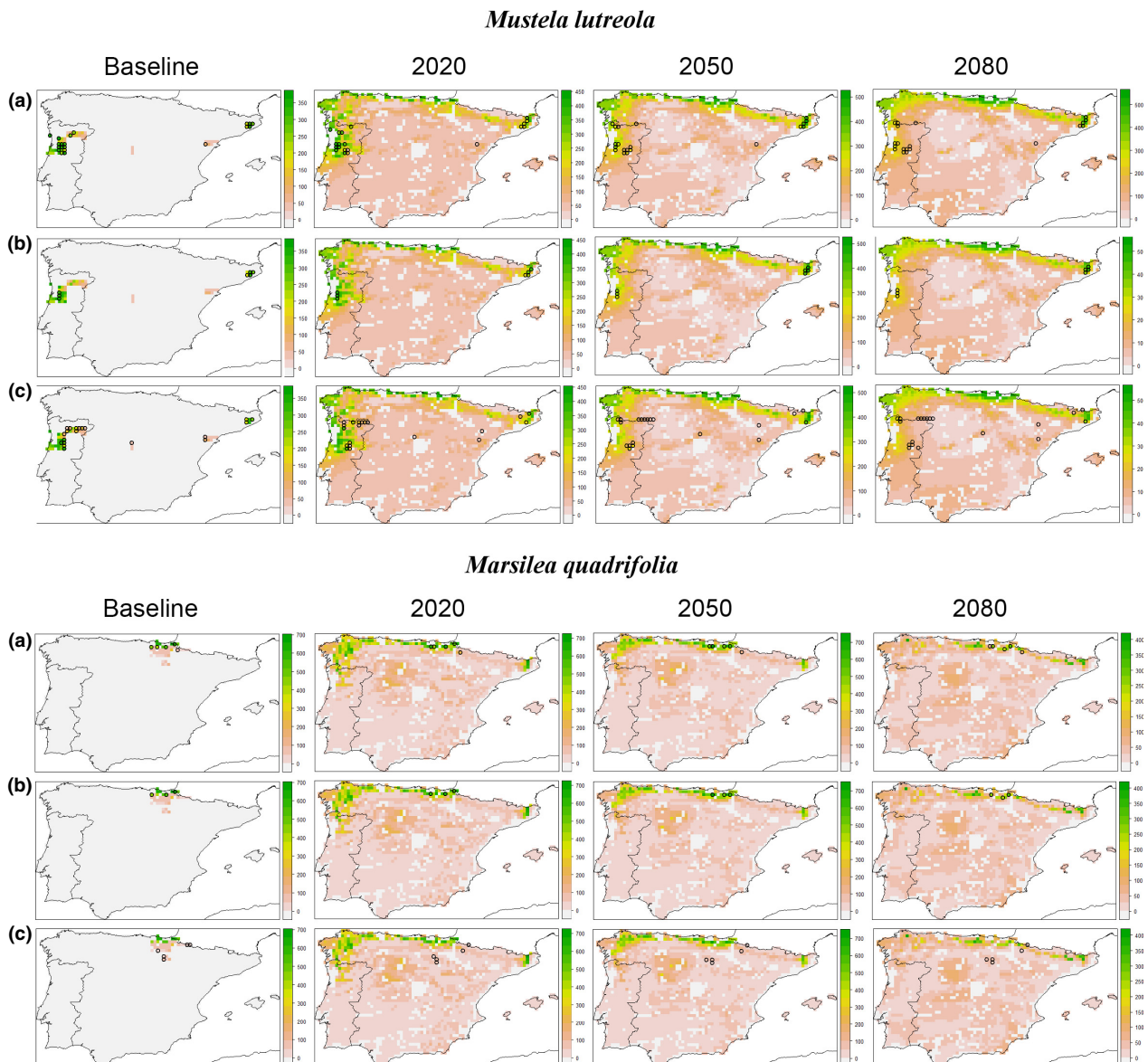
Mustela lutreola

Baseline   2020   2050   2080

(a)

(b)

(c)

Marsilea quadrifolia

Baseline   2020   2050   2080

(a)

(b)

(c)

Fig. 4. Climate-change dispersal corridors for *Mustela lutreola* and *Marsilea quadrifolia*, under the A1FI climate scenario in Iberian Peninsula with 2080 as time horizon, using a budget of 18 cost-units. Colours represent levels of predicted climatic suitability along time. Maps represent solutions obtained with (a) maximum-persistence model (*MaxPersistNetFlow*); (b) minimum cost with persistence targets model (*MinCostPersist*) and (c) minimum-cost model (*MinCost*). Circles represent the planning units defining climate-change corridors in each time period.

implemented. As such, the choice of the model to use depends on the specific goals, socioeconomic constraints and data available. For example, the *MinCost* model is suited for the cases where the link between the modelled climate suitabilities (or probability, or favourability) (Liu, White & Newell 2013) and population dynamics is not sufficiently strong to be used as a surrogate of local persistence of species (for discussion see Araújo, Williams & Fuller 2002; Araújo, Williams & Turner 2002) (Table 3). In such cases, decision-makers might prefer to use raw data or projections of species' presence and absence (bearing in mind that projected presence and absence maps are typically derived from a gradient of suitability converted into a binary format). The *MaxPersist* model is arguably more appropriate when the conservation of an overall set of species is more important than individual species persistence objec-

tives. This planning may occur, for example, if the focal species belong to a community which is expected to respond similarly to climate change (Drielsma *et al.* 2014; but see Baselga & Araújo 2009). In contrast, if strict requirements exist for every species owing to their idiosyncratic responses to climate change and when species-specific persistence evaluations are reliable, then *MinCostPersist* is likely the most suitable model to be used (Table 3).

The conservation models described herein are constrained by several factors common to all data-hungry spatial conservation planning approaches. Chiefly, these approaches are highly reliant on species distributions data, which are often quite sparse, or on inferences of species distributions obtained from models (either mechanistic, correlative or hybrid), which can carry significant uncertainties. Correlative bioclimatic models

Table 3. Reference cases that best suit the distinct model procedures for the identification of 'climate-change corridors' departing from bioclimatic modelling data. *MinCost*: minimum-cost dispersal corridors; *MaxPersist*: maximum-persistence corridors; *MinCostPersist*: minimum-cost corridors with persistence targets

Model	Reference case
MinCost	• When local suitability data are unavailable or highly uncertain for the analysed species, reporting the potential colonisation of areas with a binary index may be an alternative; • Species' dispersal kernels are not available, considering a binary dispersal index (dispersal rate or maximum dispersal distance) may be considered; • Targets are defined in terms of surface area covered by each species along time.
MaxPersist	• Local suitability data for the analysed species are available, and uncertainty is low or it may be accurately integrated within a cost index; • A dispersal kernel may be reliably developed for each species; • Reliable persistence function depending on local suitabilities and dispersal processes is available; • When one aims to preserve a set of species as an all, and when 'sacrificing' some particular species is not a concern; • Targets are defined in terms of surface area covered by each species along time. *MaxPersistNetFlow* • It delivers optimal solutions[a] • Solutions require higher computational time to be obtained comparing with *MaxPersistCorridor*[a] *MaxPersistCorridor* • Suboptimal solutions are admissible[a] • Solutions require less computational time to be obtained comparing with *MaxPersistNetFlow*[a]
MinCostPersist	• Local suitability data for the analysed species are available, and uncertainty is low or it may be accurately integrated within a cost index; • A dispersal kernel may be reliably developed for each species; • Reliable persistence function depending on local suitabilities and dispersal processes is available; • Targets are defined as levels of persistence within the geographical space and time horizon that each species needs to attain within the selected corridors. Given that persistence indices are not directly translated in terms of total covered area, the feasibility of getting all the persistence targets is hardly assessed. If unfeasible solutions occur relaxing the targets for those species that determine unfeasibility may enable solutions to be obtained.

[a]See Appendix S3 for a testing case of *MaxPersistNetFlow* and *MaxPersistCorridor* algorithm performances.

(also known as species distribution models and ecological niche models) are widely used and are particularly attractive, owing to their simplicity, to inferring distributions for multiple species. However, being correlative, they cannot effectively handle extrapolations, whereby models are forced to project distributions beyond the range of values used to train them (Thuiller *et al*. 2004). Such extrapolations are frequently observed, when models project distributions under climate change (e.g. Araújo *et al*. 2011). Furthermore, by estimating bioclimatic envelopes from correlations between snapshots of species distributions and abiotic factors, these models do not explicitly handle complex biological and ecological factors, including species interactions, evolution, and intraspecific trait variation among others (Buckley *et al*. 2010). Factors are also determinant in driving biodiversity conservation assessments. Several of the limitations associated with correlative bioclimatic models also apply to mechanistic models, hence to hybrid approaches too. For example, factoring in biotic interactions and evolution within existing models of biotic responses to climate change is still beyond capacity and would be valuable improvements to develop conservation plans with high accuracy and robustness.

In contrast to biological and ecological uncertainties, algorithmic uncertainties (*sensu* Pearson *et al*. 2006) are manageable, to some extent, with spatial conservation planning tools. For instance, a variance across models can be included in the cost layer for each planning unit specifying model precision within an ensemble framework (Kujala *et al*. 2013; Lemes & Loyola 2013). Conservation plans using such 'consensus' across ensembles of models can thus be interpreted as reducing the algorithmic uncertainty of the models, thus maximising the chances that species are conserved within conservation areas. In min-cost approaches, uncertainty taken as cost is directly minimised from the objective function. In maximum benefit models, the best outcomes are obtained from a predefined admissible level of uncertainty defined as a budgetary restriction. Additionally, sensitivity analyses are recurrently used to assess the effects of distinct climatic storylines and modelling schemes (e.g. GCMs) over the effectiveness and efficiency of conservation plans (Meller *et al*. 2014). The conservation planning formulations proposed herein are also amenable to integrate flexibility among the delivered solution proposals given that they recursively deliver multiple good-quality solutions enabling alternative scenarios to be considered by stakeholders during the implementation phase (Visconti & Joppa 2015).

Besides local climate suitability, used as a surrogate for the suitability of areas for species persistence, and dispersal, overall species persistence greatly depends on species-, local- and time-specific (and often multiple) threats that are hard to model at

regional-to-continental scales (Araújo, Williams & Turner 2002). *MaxPersist* and *MinCostPersist* are highly sensitive to estimates of species persistence and therefore prone to uncertainties in the calculus of persistence probabilities. More accurate predictions of persistence can be obtained from dynamic population models that integrate regional-to-continental scale processes with local dynamics. Provided that sufficient data on the demography, ranges and traits of species exist, such models can provide estimates of species' persistence that are, at least theoretically, more robust than that of correlative approaches (e.g. Akçakaya *et al.* 2006; Anderson *et al.* 2009; Fordham *et al.* 2013b). Additionally, the persistence metrics used to evaluate corridor effectiveness may be replaced by other index considering other sources of extinction risk propagated through time (e.g. a mixture of spatial and demographic factors obtained from metapopulational models as used in Fordham *et al.* (2013a) and Pearson *et al.* (2014)).

Here we have tested three alterative models to the climate-change corridor problem for biodiversity. In our prototypical and very simple case study, all solutions were obtained in less than 20 s. However, with more realistic assessments involving more species, optimal solutions will be hard to achieve either with reasonably time or with standard computational resources (especially for the more complex *MaxPersist* and *MinCostPersist* problems). This is where heuristically driven selection tools, as *Zonation* and *Marxan*, gain relevance, given that their algorithms do not run for full optimality but make good trade-offs between processing time and solution suboptimality (Rodrigues & Gaston 2002; Moilanen 2008). For this reason, we have developed formulations for the *MaxPersistCorridor* and *MinCostPersist* problems that use smaller sets of candidate corridors for selection, thus reducing the 'size' of the problem and providing users the control of processing times and solution suboptimality.

We also tested the performance of the suboptimal *MaxPersistCorridor* solutions against the full optimal *MaxPersistNetFlow* ones (Appendix S3). Species persistence in the *MaxPersistCorridor* solutions approximated the optimal solution, especially for the hardest problems to solve (i.e. problems depending on tighter budgets). Although generalisations of these results to other implementations should be taken with care, the near optimality of the *MinCostPersist* solution, coupled with its speed, is particularly attractive for solving large biodiversity conservation problems.

Conclusion

Choosing the best conservation model requires a full understanding of the decision context in which priority areas are to be chosen. Understanding this context requires a clear statement of the scope of decisions to be made, intended objectives and an assessment of the trade-offs among articulated conservation objectives (Margules & Pressey 2000). For example, should conservation plans be guided by financial factors or by ecological outcomes? Which should be the main subject of a conservation plan, species taken independently or a coherent pool of species?

With this study, we have widened the mathematical-based optimisation toolbox available for decision-makers. We deliver quite flexible tools that can be implemented within general-purpose integer programming solvers (e.g. *CPLEX, NEOS, R-CRAN, MatLab*) and that can accommodate a wide array of practical real-world problems. If appropriately used, they have great potential to increase the likelihood that adequate conservation investments are made and contribute to preserving biodiversity within a dynamic and complex world.

Acknowledgements

Data accessibility

Data from this analysis are available in Supporting Information (Data S1).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Literature review.

Appendix S2. Species distribution modelling, species' dispersal models, planning-unit cost layer and choice of conservation targets.

Appendix S3. Tests to compare performance of *MaxPersistNetFlow* against *MaxPersistCorridor* solutions.

Appendix S4. Description about file structure with source code and case study data.

Fig. S1. Georeferenced planning-unit cost layer.

Fig. S2. Distribution of the of the 2,500 top ranked persistence scores within corridors for *Mustela lutreola*, and *Marsilea quadrifolia*.

Fig. S3. Persistence scores for *Mustela lutreola*, and *Marsilea quadrifolia*, using three corridor selection models.

Data S1. Source code and case study data to formulate and solve *MinCost*, *MaxPersistNetFlow*, *MaxPersistCorridor* and *MinCostPersist* climate change corridor models.