Shifting protected areas: scheduling spatial priorities under climate change

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Summary

1. Conservation planning decisions are constrained by three important factors: budgets are limited, important areas for biodiversity compete for space with other uses, and climate- and land-use changes are affecting the distribution of life thus compounding existing threats to biodiversity. Decisions about locating and allocating resources for conservation in such complex and dynamic world are far from trivial, with apparently optimal decisions in the present being potential suboptimal in the future.

2. We propose a methodological framework for the dynamic spatial prioritization of conservation areas that optimizes long-term conservation goals under climate change. This approach involves a sequential scheduling of conservation areas designation, followed by the release of some areas when they stop contributing to the specified long-term conservation goals. The usefulness of the proposed approach is demonstrated with a case study involving ten species in the Iberian Peninsula under severe scenarios of climate change, but the framework could be applied more broadly.

3. Species persistence under climate change is enhanced by the dynamic spatial prioritization strategy that assumes area release. With such strategy, the long-term persistence of species is consistently higher than expected with no release of redundant areas, particularly when the budgets to acquire and manage conservation areas are small. When budgets are small, long-term persistence of species might only be achieved when the release of previously selected areas is considered alongside the selection of new areas.

4. *Synthesis and applications.* Given that conservation budgets are typically small, conservation strategies involving the release of some underperforming areas might be required to achieve long-term persistence of species. This should be the case when climate change forces species to move out of current protected areas with other areas becoming important to meet conservation objectives. Implementing such dynamic prioritization approach would require a paradigm shift in conservation planning because conservation areas, once selected, are rarely released. Dynamic selection of areas also involves risks that should be considered in a case-by-case situation.

Key-words: connectivity, decision theory, degazetting, dispersal, efficiency, network flows, optimization, protected areas, species persistence, systematic conservation planning

Introduction

Biodiversity conservation is strongly reliant on the classification and management of networks of protected areas.

However, such networks are commonly considered static because areas that have been classified as protected are almost never declassified (see for review Mascia & Pailler 2011). Although protected areas have proven to be remarkably successful at buffering species against historical drivers of populations decline, such as habitat loss,

fragmentation, over-hunting and resource depletion (UNEP 1992), many species are likely to be forced out of protected areas under scenarios of climate change (Halpin 1997; Araújo *et al.* 2004; Pressey *et al.* 2007). Indeed, models project that several protected areas will lose suitable habitats for species of high conservation concern (e.g. Hole *et al.* 2009; Kharouba & Kerr 2010; Araújo *et al.* 2011; Virkkala *et al.* 2013). To address this challenge, researchers and conservation bodies recognize that new conservation areas will need to be designated in future (Hannah & Salm 2003; Araújo 2009b). However, conservation budgets are limited, and classifying new areas to buffer against the negative effects of climate change on species can be extremely expensive (Hannah *et al.* 2007; Wise *et al.* 2012). Thus, there remains a question as to whether efficient strategies can be devised so that long-term conservation targets are met while keeping budgets under control.

Sophisticated methods for spatial conservation planning have been developed to account for the shifting distributions of species under climate change (Williams *et al.* 2005; Phillips *et al.* 2008; Vos *et al.* 2008; Saura, Bodin & Fortin 2014). These methods target areas that remain climatically suitable across a given period of time (i.e. the so called 'stay at home' populations) and areas that provide linkages (i.e. dispersal pathways) between climatically suitable areas in the present and future (see for review Araújo 2009a). Spatial conservation prioritization methodologies that take climate change into account often do so through by incremental addition of new sets of areas to existing conservation areas systems. However, in a dynamic world in which species distributions are constantly reshuffled, it is possible that some conservation areas might become redundant as species move away from them. When this is the case, dynamic spatial prioritization strategies can be devised to identify sets of areas that optimize conservation benefit across several periods of time. Efficiency (i.e. meeting conservation targets at minimum cost) can then be achieved by scheduling the selection and release of areas following the needs of species conservation across the entire planning period.

The idea that underperforming conservation areas can be replaced by new areas has been proposed before (Strange, Thorsen & Bladt 2006; Rayfield *et al.* 2008; Fuller *et al.* 2010). However, to our knowledge, only Strange *et al.* (2011) implemented this concept within the specific context of climate change. In their approach, Strange *et al.* (2011) applied stepwise heuristic decision rules to optimize distinct conservation objectives (e.g. maximization of species coverage, maximization of climatic suitability, minimization of total cost and minimization of conversion risk) for every period of time considered. However, their model does not explicitly consider the distances that species need to travel between areas.

Here, we tackle the specific spatial conservation prioritization problem arising when selection of new conservation areas is considered alongside the possibility of release of existing conservation areas. Unlike Strange *et al.* (2011), our approach was developed to retrieve global optimal solutions and to explicitly account for varying dispersal requirements of species. With our approach, priority areas are identified in such a way as to allow species to track suitable climates through dispersal pathways; this is done by combining projections of local climate suitability together with scenarios of species' dispersal and thereby providing rough phenomenological estimates of species persistence (Araújo & Williams 2000; Araújo, Williams & Fuller 2002). Ultimately, the areas required to maximize species' persistence for a given time horizon are selected as part of a scheduling plan that identifies the periods in which these areas are to be designated and managed for conservation. The selection process is constrained by the available budget and solutions assuming different budgets can be compared.

To illustrate the framework, we implement it for ten species in the Iberian Peninsula and Balearic Islands. We demonstrate that the proposed dynamic spatial prioritization approach meets conservation targets more effectively under climate change than the continued accretion of areas, particularly when budgets for conservation are restricted. We conclude that adequately adapting conservation policies to climate change requires a paradigm shift. Specifically, planners need to adopt a long-term view and accept that under budgetary constraints the release of conservation areas that become redundant at some point in time might be required if new conservation areas are to be designated to meet conservation targets.

Materials and methods

The proposed framework for dynamic spatial conservation planning is a repeatable and transparent approach to assist planners and policy makers in anticipating future conservation prioritization needs. The framework is composed of five tasks (Fig. 1). The details of each task are presented below.

TASK 1 – HABITAT SUITABILITY

The framework requires that changes in habitat suitability are first modelled. Habitat suitability can be modelled in several ways, but often projections can be obtained with models that infer changes in climate suitability from correlations between species distributions data and climate variables (Thuiller, Araújo & Lavorel 2004; Triviño *et al.* 2011). When the response variable includes representative samples of presence and absence records (rather than presence-only records), models yield predictions of probabilities of occurrence, and these have properties that make them particularly amenable for spatial conservation prioritization (Williams & Araújo 2002). Projections are then made for each species for a baseline period and for a sequence of *t* periods in future. Apart from these correlative methods, other modelling techniques are available for projecting climate suitability over time: physiologically based mechanistic models (Buckley *et al.* 2010; Araújo *et al.* 2013) and coupled niche-metapopulation models (e.g. Brook *et al.* 2009; Fordham *et al.* 2013).
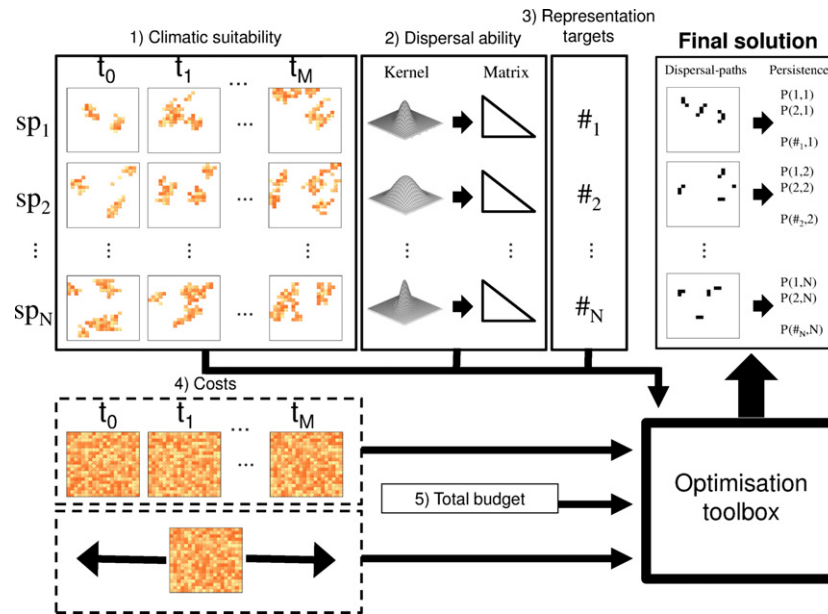
Fig. 1. Framework for selecting areas to assist species persistence under climate change. The framework integrates several components. (1) Climatic suitability: for each species (sp_1, sp_2,...sp_N), maps of suitable climate are produced for the time periods under analysis (t_0, t_1,...,t_M). (2) Dispersal ability: for each species, a kernel of dispersal success as a function of distance is adopted; after translation to a map, the kernel produces a matrix relating each pair of planning-units in terms of dispersal success. (3) Amount of area to be targeted for each species over time: the number of planning-units to select in each time period (#1, #2,..., #N). (4) Costs: for the dynamic spatial conservation prioritization strategy, the cost of designating each planning-unit is required for each period; for the static strategy, the cost of designating each planning-unit in the long term is required. (5) Total budget: the financial effort to designate planning-units for the time horizon considered. The outputs of (1 to 5) are entered into 6) the optimization toolbox: the formulation of dynamic and static selection strategies and algorithms to obtain solutions. The outputs from this framework are the areas to be selected for each species and their respective species persistence index, $P(.,.)$.

The spatial predictions of species distributions under climate change are subject to uncertainty arising from algorithms and methods (see for review Heikkinen *et al.* 2006), from aspects of the ecology of organisms (e.g. Brotons *et al.* 2004) and from semantic and conceptual interpretations (e.g. Araújo & Peterson 2012). Altogether these uncertainties are known to have an important impact in spatial conservation prioritization (Loiselle *et al.* 2003; Kujala *et al.* 2013). Predictive uncertainty in models is usually quantified or controlled for scenarios of future emissions of greenhouse gases, global models of atmosphere-ocean circulation, species distribution models and rules to transform habitat suitability/probabilities into species presence/absence (Beaumont, Hughes & Poulsen 2005; Diniz-Filho *et al.* 2009; Nenzén & Araújo 2011). Uncertainties arising from extrapolating species–climate relationships beyond the range of values used to parameterize the model have also been considered (Thuiller *et al.* 2004; Fitzpatrick & Hargrove 2009). To account for such uncertainties in models of species distributions, different projections can be generated – the ensemble forecasting approach (Araújo & New 2007) – and combined using a variety of consensus methodologies (Garcia *et al.* 2012).

The use of ensembles in conservation planning is still in its infancy. The simplest implementation involves using the consensus of several projections in the decision process (e.g. Araújo *et al.* 2011). There is some evidence from independent evaluation of models that consensus projections increase the predictive accuracy of models with regards to individual projections (Araújo *et al.* 2005b), although there is also the possibility that this may not always be true. However, in some cases, planners might like to explore multiple conservation planning scenarios thus characterizing solutions with varying levels of uncertainty. One option is to repeat the spatial conservation prioritization process for a reduced number of alternative consensus solutions (sensu Araújo, Thuiller & Pearson 2006). A more computer-intensive approach is to calculate conservation solutions for every individual model projection and explore the resulting range of uncertainties a posteriori. Yet, another possibility is to weight model outputs according to the degree of 'certainty' of their results. Let us consider that the range of predicted suitability values from ensemble for each area range from s_{min} to s_{max}. One could assign to each area a suitability value randomly selected in the interval [s_{min}, s_{max}], but giving higher probability to lower values (e.g. using a beta distribution, $Beta(\alpha = 1, \beta \geq 2)$). This would make areas with higher uncertainty in suitability less likely to be selected (see also Moilanen *et al.* 2006). Here, because the focus is on the illustration of the general framework rather than on providing a full examination of uncertainties of the models, we explore conservation scenarios for a single consensus solution.

TASK 2 – SPECIES DISPERSAL ABILITY

To track climate change, species need to reach suitable habitats through dispersal as they become available away from their historical locations. Three conditions are required for successful dispersal: species have to have traits of mobility that are sufficiently effective to allow the tracking of climate change (Hughes *et al.* 1994), dispersal distances need to be within the constraints imposed by the climate change velocity (Higgins & Richardson 1999), and the landscape matrix needs to be sufficiently permeable to enable dispersal (Collingham & Huntley 2000). Because

rigorous species' dispersal kernels for short- and long-distance dispersal are generally unavailable, coarse generalizations are inevitable (Pearson & Dawson 2005). In these cases, sensitivity analysis should be performed, and the patterns obtained under different choices should be evaluated (McDonald-Madden, Baxter & Possingham 2008; Beier, Majka & Newell 2009). Estimates of landscape permeability, including information on local barriers to dispersal, should also be considered when building the dispersal matrix (Alagador *et al.* 2012; Brás *et al.* 2013).

TASK 3 – SPECIES REPRESENTATION TARGETS

The number of new conservation areas required for species persistence under climate change should ideally be defined species by species (Bottrill *et al.* 2008). However, when species-specific conservation needs are lacking priorities can be defined equally across species. In such cases, a fixed number of area or pathways might be defined for all species (e.g. Williams *et al.* 2005).

TASK 4 – COSTS AND BUDGET

The simplest treatment of cost is to assume a linear positive relationship between cost and area (Frazee *et al.* 2003). In practice, the cost–area relationship does not often fit a perfect regression line and more direct assessments of conservation costs including land acquisition, management or opportunity costs are desirable (Adams, Pressey & Naidoo 2010; Wise *et al.* 2012). Similarly, if conservation budgets are known, a priori spatial conservation planning decisions may balance costs and budgets appropriately through time.

TASK 5 – OPTIMIZATION

The proposed framework optimizes the persistence of a set of species for a given horizon of time by defining a sequence of planning-units (i.e. dispersal pathways) that is required to allow species to track suitable climates. Because persistence is the outcome of several factors acting on individual species (Williams & Araújo 2002), we developed a metric of persistence for each species within a dispersal pathway, as follows:

$$P(path, sp) = s_i^{0,sp} \times d_{ij}^{sp} \times s_j^{1,sp} \times d_{jk}^{sp} \times s_k^{2,sp} \times d_{k.}^{sp} \times \ldots \times d_{.l}^{sp} \times s_l^{t,sp}$$

$$\text{eqn 1}$$

where $s_i^{0,sp}, s_j^{1,sp}, s_k^{2,sp}, \ldots, s_l^{t,sp}$ are the climate suitabilities of species, sp, within the pathway formed by planning-units, $i, j,\ldots l$, in their respective periods, t, and $d_{ij}^{sp}, d_{jk}^{sp}, d_{k.}^{sp}, \ldots, d_{.l}^{sp}$ represents the species dispersal success when moving between planning-units selected for consecutive time periods.

This persistence metric ranges from zero to one. A pathway with a persistence score of zero presents either a planning-unit with null suitability in some period or a null expectation for species to disperse between the planning-units selected for consecutive periods. Pathways with persistence scores equal to one include planning-units with maximum climate suitability and with no risk of dispersal failure (e.g. if dispersal success is negatively correlated with movement distance, maximum success implies no dispersal; in such cases, pathways with a maximum persistence are composed of one planning-unit retaining maximum suitability and in which the species persists over time, that is, local refugia).

We formulated the spatial conservation prioritization problem as a multicommodity network flow problem. Here, the persistence of all species within a number of non-intersecting pathways (to be targeted for each species) is to be maximized (eqn 2) given a fixed conservation budget for the time horizon under consideration.

$$\max \Pi_{sp}\Pi_{path}P(path, sp) \qquad \text{eqn 2}$$

Two spatial conservation prioritization strategies were formulated. One represents the current static conservation approach in which planning-units once selected are retained perpetually for conservation. The other (hereafter termed dynamic) allows the planning-units to be released from conservation management if their replacement by new areas results in higher combined persistence of the targeted species (see Appendix S1, Supporting Information for complete formulations of the two versions).

CASE STUDY

To illustrate the framework, we chose a small sample of species occurring in the Iberian Peninsula and Balearic Islands that represent different clades, levels of threat and exposure to climate change (Table 1). The sample of species was chosen for illustration of the framework, but the concepts and methods proposed are applicable to any biological system.

The study region was divided into 2310 100-km^2 planning-unit squares, and climate suitability for each species was estimated for four periods of time (baseline, 2020, 2050 and 2080), under two IPCC (Intergovernmental Panel for Climate Change) greenhouse gas emission scenarios (Nakicenovic *et al.* 2000) (A1FI and B1). Estimates of habitat suitability through time were obtained from an ensemble of seven bioclimatic envelope models and three atmosphere-ocean global circulation models (for the future periods) published elsewhere (see Araújo *et al.* 2011). Models were fitted using a combined data set (Williams *et al.* 2000) of presence–absence for European amphibian and reptiles (Gasc *et al.* 1997), birds (Hagemeijer & Blair 1997), mammals (Mitchell-Jones *et al.* 1999) and plants (Jalas & Suominen 1972–1996). Presence–absence data were recorded in 2500-km^2 planning-unit squares (i.e. 50 × 50 km grid cells) and climate variables at the same resolution were obtained and averaged across 1961–1990 (baseline period). Specifically, four climatic variables were used: mean annual growing degree days (>5 °C), mean temperature of the coldest month (°C), mean total annual precipitation (mm) and a moisture index taken as the ratio of mean annual actual evapotranspiration over mean annual potential evapotranspiration (provided by the Climate Research Unit at the University of East Anglia, Mitchell *et al.* 2004). We then projected the bioclimatic envelope models to 100-km^2 planning-units (i.e. 10 × 10 min grid cells) using available downscaled climatic information for the baseline period and for future time periods (1990–2020 (2020), 2020–2050 (2050) and 2050–2080 (2080) averaged data) under two alternative IPCC socio-economic scenarios: A1FI and B1 (for discussion of the downscaling approach see Araújo *et al.* 2005a).

We had no access to empirical estimates of dispersal rates for the selected species; therefore, theoretical kernel curves were generated to reflect the dispersal success of species moving from a source to a target area within a given period of time (e.g. Saura, Bodin & Fortin 2014). For each species, we used simple rules to

Table 1. The species under analysis. The general profiles of the selected species: scientific name and abbreviation, taxonomic position, conservation status, distribution pattern, predicted impacts of climate change for 2080 under the A1FI IPCC's AR4 scenario (winner for the species predicted to gain climatic suitability and loser for the species predicted to lose climatically suitability, see Araújo *et al.* 2011) within (PAs) and outside the protected areas (oPAs) of Portugal and Spain; the adopted value for maximum dispersal distance in 30 years (*Dmax*); and the percentage of the climatically suitable area in the baseline period that is covered by the 20 pathways targeted for each species (Rel area)

Name (Abbreviation)	Taxa	Status and Distribution	Climate (PAs/oPAs)	*Dmax* (km)	Rel area *(%)*
Pleurodeles waltl (Pwa)	Amphibia	Near threatened *	Loser/Loser	5	1·97
Natrix maura (Nma)	Reptilia	Endemic in Iberia and Marrocos	Loser/Loser	20	1·11
Regulus regulus (Rre)	Aves	Winter	Winner/Winner	50	3·93
Sorex coronatus (Sco)	Mammalia	Endemic in Western-Central Europe	Winner/Loser	20	5·56
Crocidura russula (Cru)	Mammalia	Appendix III [†]	Winner/Loser	30	1·25
Mustela lutreola (Mlu)	Mammalia	Critically endangered * and Annex II [‡]	Loser/Loser	40	46·51
Marsilea quadrifolia (Mqu)	Brassicaceae	Annex II [‡]	Loser/Loser	20	34·48
Quercus petraea (Qpe)	Marsileaceae	SW range in Iberia	Loser/Loser	50	5·08
Silene legionensis (Sle)	Fagaceae	Endemic in Iberia	Loser/Loser	40	3·70
Draba dedeana (Dde)	Caryophyllaceae	Endemic in Europe	Winner/Loser	20	7·14

*IUCN Red List of Threatened Species. Version 2009.
[†]Council Decision (82/72/EEC).
[‡]European Community Directive (92/43/EEC).

define maximum dispersal distances (*Dmax*) taking into account traits such as body size and mode of dispersal (Table 1 and Appendix S2 (Supporting Information) for a comprehensive description on how maximum dispersal distances were derived). Variation in the dispersal success with distance, d_{ij}^{sp}, was then modelled using a negative exponential function such that:

$$d_{ij}^{sp} = \begin{cases} e^{-\alpha \cdot \frac{dist(i,j)}{Dmax(sp)}} & , \text{if } dist(i,j) \leq Dmax(sp) \\ 0 & , \text{if } dist(i,j) > Dmax(sp) \end{cases} \qquad \text{eqn 3}$$

where $dist(i,j)$ is the distance (centre-to-centre) between planning-units *i* and *j*. Three curves with varying α-values were considered (Fig. S1, Supporting Information). The main analysis was conducted using an intermediate α-value, whereas the lower and higher α-values were used for the sensitivity analysis. We chose 20 dispersal pathways for each species as a representational target to be attained across time. This value enabled that 1% to 50% of the available suitable areas (i.e. non-zero suitability) for each species occurring in the baseline period are devoted to conservation in each time period (Table 1).

We selected different budgets for the selection of dispersal pathways. The budgets ranged from the minimum required to meet the target of 20 pathways per species (restricted budget) to a budget that imposes no restrictions on the selection of planning-units (unlimited budget), with selection being solely determined by the persistence metrics (see Appendix S1, Supporting Information).

Conservation costs per planning-unit at such a large grain size (i.e. 100 km[2]) are typically difficult to obtain with precision. Assuming that conservation management is less expensive for planning-units already committed to conservation programmes, we estimated the cost of conserving a planning-unit *i*, c_i, as the percentage of its surface area outside the existing protected areas (Araújo *et al.* 2011; Alagador *et al.* 2012; Fig. S2a, Supporting Information).

Lastly, to ensure that the targeted areas were not heavily degraded by human activities, we removed from the set of candidate areas for selection the planning-units that presented a high degree of natural habitat conversion. The Human Footprint

Index was used to measure such an effect (Sanderson *et al.* 2002). Although Human Footprint Index is provided at a 1-km[2] resolution, we resampled the 'footprint values' to the 100-km[2] planning-unit resolution used herein retaining its average value. The 'footprint values' range between zero and 100, with the higher values corresponding to higher human pressure. We used 50 as a threshold to classify the planning-units as highly converted (Alagador *et al.* 2012). Of the 2310 planning-units, 1932 were retained in the analysis (Fig. S2b, Supporting Information).

We assessed the performance of the static and the dynamic spatial conservation prioritization strategies by comparison of the objective-function values obtained (eqn 2) for a range of budgets. The planning-unit costs associated with the static strategy were estimated directly from c_i, and they correspond to the theoretical investment necessary to acquire and manage an area in the long term. For the dynamic strategy, the planning-unit costs were adapted to reflect a temporary 30-year investment (i.e. the time interval between action periods). 'Temporary costs', c_i^t, were defined using four alternative modes by varying their relationship with the corresponding long-term cost, c_i:

$$c_i^t = c_i/4 \qquad \text{eqn 4}$$

$$c_i^t = 1.1 \times c_i/4 \qquad \text{eqn 5}$$

$$c_i^t = 0.9 \times c_i/4 \qquad \text{eqn 6}$$

$$c_i^t = U(0.9, 1.1) \times c_i/4 \qquad \text{eqn 7}$$

Equation 4 refers to a scenario in which the cost to temporarily conserve planning-unit *i* in (four) successive periods of time equals its respective 'long-term conservation cost'. Equations 5 and 6 refer to scenarios in which the cost of acting temporarily over time is 10% higher and 10% lower than the long-term cost, respectively. Lastly, equation 7 presents a scenario in which the 'temporary costs' randomly differ from the corresponding 'long-term costs'. The ratio of temporary costs to 'long-term costs' was drawn from a uniform distribution between 0·9 and 1·1 (noisy 'temporary costs').

We evaluated the extent to which persistence estimates and the areas to select under the dynamic strategy were robust to variation from different sources. Specifically, we generated solutions for all the combinations of future climate scenarios (two levels: A1FI and B1), budget scenarios (two levels: restricted and unlimited), planning-unit costs (four levels: balanced, +10%, −10%, and random noise) and species' dispersal kernel curves (three levels: low, intermediate and high α-values), for a total of 48. We used Cohen's kappa statistic (κ) for each source of variation and each time period to measure agreement between the corresponding pairs of solutions generated from all combinations of the levels. We also assessed the variation of the species-combined persistence within the targeted areas (i.e. the optimized function in equation 2) for each factor level using Wilcoxon signed-rank tests using the *R* statistical software (http://cran.r-project.org).

Results

The dynamic spatial conservation prioritization strategy achieved greater overall persistence for the ten species analysed than the static prioritization strategy. This was true for all tested budgets. The trend for improved persistence with the dynamic strategy was consistent for all but one planning-unit cost scenario. When planning-unit 'temporary costs' were established 10% above the corresponding 'long-term acquisition costs', the dynamic strategy was less effective in achieving species' persistence than the static selection for budgets higher than approx. 40·00 cost-units. Generally, the marginal gains from using a dynamic approach were greater for the smallest budgets (Fig. 2). With budgets lower than 36·36 cost-units, only the dynamic strategy achieved the established species representation targets. When analysing the expected persistence of individual species, we found that the benefits of dynamic areas over static ones were not always consistent: for a few 'species × budget' assessments, the areas selected with the static strategy yielded higher persistence (Fig. S3, Supporting Information).

Under the minimum budget scenario, the static spatial conservation prioritization approach led to selection of 58 planning-units that remained fixed over the time period analysed (Table 2 & Table S1, Supporting Information, Fig. 3 and Fig. S4, Supporting Information). With the dynamic approach, the most restricted budget (68% of the most restricted budget for the static conservation prioritization approach) resulted in more planning-units to acquire/manage yet with smaller average conservation costs that decreased with time. The turnover in selected conservation areas also decreased with time such that 40% of the area is released from the baseline period in contrast to the 10% of area being released from the 2050 solution.

Differences between solutions from static and dynamic conservation prioritization approaches were not clear cut when no budgetary limits existed (Table 2 & Table S1, Supporting Information), even though a distinct trend in the total area conserved was recorded. The total area increased with the static strategy, particularly from the baseline period to 2020, whereas a slight decrease in total conserved area
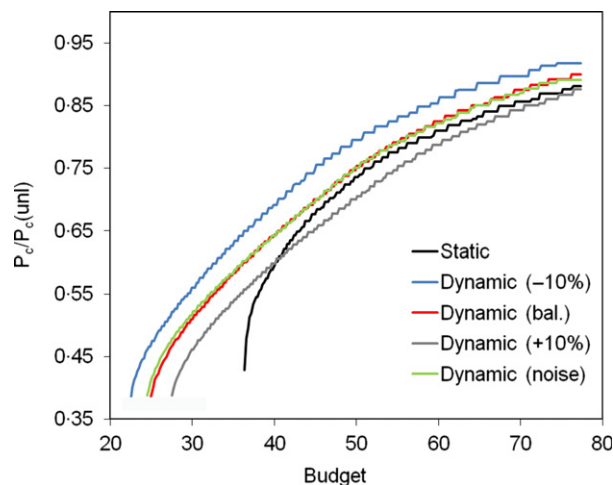
Fig. 2. Variation of the combined species persistence (measured as a fraction of the maximum attained persistence obtained with an unlimited budget) achieved for the ten species under analysis within their respective sets of conservation areas (dispersal pathways). The solutions were obtained by applying a range of budgets for planning-unit acquisition and adopting static and dynamic spatial conservation prioritization strategies. Different planning-unit cost scenarios were produced to reflect imbalances of different extents between the 'long-term acquisition cost' and the cost to temporarily acquire conservation areas (bal, balanced costs; +10%/−10%, the 'temporary acquisition cost' is 10% higher/lower than the 'long-term acquisition cost'; noise, the 'temporary acquisition cost' differs by a random noise from the balanced cost).

was recorded with the dynamic strategy. As above, the turnover of areas was most pronounced in the baseline period.

Variation in the available budget produced the most dissimilar solutions for all time periods (Fig. S5a, Supporting Information) with significantly different levels of combined persistence achieved (Fig. S5b, Supporting Information). That is, with a restricted budget, solutions were on average 65% less effective in attaining species persistence than solutions with no budgetary limitations (Wilcoxon signed-rank test: $P < 0.001$). Differences between prioritized areas and their timing of selection were almost negligible when comparing future climatic scenarios ($0.86 < $ averaged-κ < 0.87: Fig. S5a, Supporting Information), but the combined species persistence was significantly higher for the B1 scenario than for the A1FI scenario (Wilcoxon signed-rank test: $P < 0.001$). Lastly, the use of distinct planning-unit costs and dispersal kernels did not result in substantially different area prioritization schedules and combined species persistence.

The positive budget–persistence relationship was particularly noteworthy for some of the species (*Draba dedeana* and *Silene legionensis*), the persistence of which increased significantly from zero when the available budget increased from restricted to unlimited (Fig. 4). However, for *Mustela lutreola* and *Marsilea quadrifolia*, even an unlimited budget did not allow the selection of areas that would ensure species persistence substantially above zero. These results stemmed from three non-mutually exclusive circumstances:

Table 2. Summary of solutions obtained using the dynamic spatial conservation prioritization strategy for different time periods under two budgetary (Res., restricted; Unl., unlimited) and two future climate (A1FI; B1) scenarios. The summarized information is expressed in terms of the number of planning-units selected in each time period (Sel.) and released from each time period (Rel.) and their associated average 'temporary conservation costs' (Avg. cost)

| Budget | Climate | Effect | Baseline | | 2020 | | 2050 | | 2080 |
			Sel.	Rel.	Sel.	Rel.	Sel.	Rel.	Sel.
Res.	A1FI	PUs	74	30	71	19	66	7	61
		Avg. cost	0·128	0·232	0·104	0·230	0·07	0·240	0·058
	B1	PUs	75	30	72	19	68	7	63
		Avg. cost	0·126	0·23	0·102	0·230	0·07	0·230	0·055
Unl.	A1FI	PUs	183	20	178	8	173	1	173
		Avg. cost	0·228	0·227	0·224	0·250	0·222	0·250	0·222
	B1	PUs	181	22	175	1	175	1	175
		Avg. cost	0·227	0·244	0·222	0·250	0·222	0·250	0·222
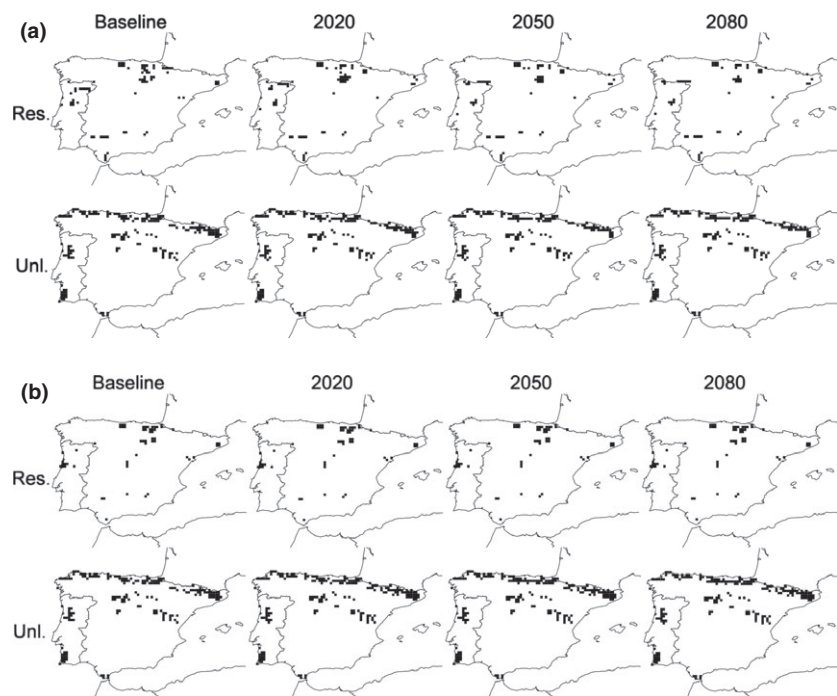
Fig. 3. The areas selected (dark planning-units) for the maximization of species persistence under the A1FI future climate scenario using (a) a dynamic strategy and (b) a static spatial conservation prioritization strategy using two budgetary scenarios (Res., restricted; Unl., unlimited). The solutions were obtained using the intermediate α-value from species dispersal kernel curves.

(i) the omission of highly suitable areas in the Iberian Peninsula in some of the time periods analysed, (ii) if existing, the areas predicted to be suitable in future were distant from the baseline-period species' ranges, and (iii) the species need to disperse continuously over time to track suitable areas (Fig. S6, Supporting Information).

The results also indicated that, with restricted budgets, persistence varied markedly across selected pathways for some of the species because poor performing pathways for one species may benefit the persistence of some other species.

Discussion

Climate change is already affecting phenology, and distributions of many species (Walther *et al.* 2002; Parmesan & Yohe 2003) and greater changes are forecasted for the 21st century (Thomas *et al.* 2004; Thuiller *et al.* 2005;

Hof *et al.* 2011a). Existing conservation prioritization schemes are, by large, static, thus neglecting the possibility that the distribution of spatial conservation priorities might change as a consequence of climate- and land-use change. To address this problem, we develop a dynamic framework for scheduling spatial conservation prioritization that identifies optimal sets of areas (dispersal pathways) allowing species to track suitable climates through time and space. In contrast to other approaches for spatial prioritization under climate change (Williams *et al.* 2005; Phillips *et al.* 2008), the proposed framework allows both the selection of new conservation areas as they become necessary, and the release of existing areas as they become redundant. In our case study, the proposed framework increased the estimated species' persistence within conservation areas when compared to familiar static spatial prioritization whereby areas are slowly accumulated without redundant areas ever being released.
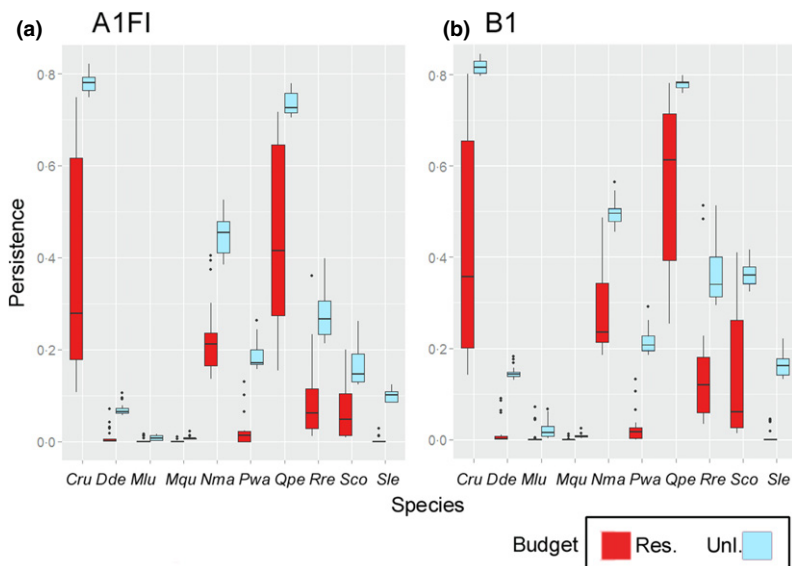
Fig. 4. Distribution of persistence of the ten species within their respective chains of conservation areas (dispersal pathways) selected using a dynamic spatial conservation prioritization strategy with a restricted and an unlimited budget for area acquisition for two future climate scenarios (a) A1FI and (b) B1. Bars delimit the 2nd and 3rd quartiles; horizontal lines mark median values; vertical lines mark 95% confidence intervals (1·5 × IQR), and; points refer to outliers. Cru, Crocidura russula; Dde, Draba dedeana; Mlu, Mustela lutreola; Mqu, Marsilea quadrifolia; Nma, Natrix maura; Pwa, Pleurodeles waltl; Qpe, Quercus petraea; Rre, Regulus regulus; Sco, Sorex coronatus; Sle, Silene legionensis.

Limitations of the static framework are particularly strong when conservation budgets are restricted because past commitments for conservation constrain the ability of planners to plan ahead and designate new areas for conservation. In contrast, if planners seek to meet conservation targets using the static approach, the overall cost will be significantly higher than with the dynamic solution (Fig. 2).

Our findings are consistent with the suggestions that gains in efficiency (conservation return by investment) are expected if existing areas that become redundant with time are traded-off by new areas that become more important for conservation (Strange, Thorsen & Bladt 2006; Strange *et al.* 2011). However, our results extend to these analyses because they account for the needs of species adaptation through dispersal under climate change and show that gains in effectiveness (species persistence) are expected in addition to gains in efficiency (for similar results without climate change see Fuller *et al.* 2010).

With the static conservation prioritization framework, sets of areas are typically set aside to ensure persistence of target species across the full time period considered. A key simplification of this approach is that these choices are made upfront (but see Hannah *et al.* 2007), which limits their utility in several ways. First, conservation budgets are generally made available in increments over time. Secondly, it is often unnecessary to designate conservation areas that are spatially remote from current populations until species or their habitats have moved sufficiently away from existing conservation areas. Thirdly, an early commitment for conservation of new areas based on species-climate change forecasts may fail to account for

uncertainties, which may result in a limited ability for adaptive responses to climate change (Keith *et al.* 2011). In practice, planners are better-off adopting adaptive management principles that would enable them to periodically review their conservation blueprints and make decisions according to the most recent population dynamics and budgetary information.

The proposed framework is essentially a tool for optimal scheduling of selection and release of conservation areas, but extensive on-the-ground research should be implemented to carefully evaluate decisions before releasing potentially redundant areas. In practice, time lags in the responses of species and communities to climate change exist. In such cases, modelled climate change impacts may overestimate the impacts that are observed on the ground and a release of protected areas might be unadvisable (Menéndez *et al.* 2006; Hof *et al.* 2011b). The microclimatic buffering of climate change (e.g. local edaphic factors, topographical complexity) can also delay or even prevent biodiversity loss (Williams *et al.* 2008). Management can also mitigate the local impacts of climate change, thus contributing to maintaining the value of areas that otherwise would lose species and communities (Heller & Zavaleta 2009; Shoo *et al.* 2013). Lastly, quantitative spatial conservation prioritization is affected by uncertainties that are difficult to quantify (e.g. uncertain estimates of changes in local climate suitability, species' dispersal abilities, conservation costs and budgets available). Whenever possible, the impacts of these uncertainties should be quantified and integrated in the analytic framework (see tasks 1, 2 and 4 in Materials and Methods). When appropriate understanding of uncertainties is

not possible, adaptive management must be put in place (Wilhere 2002). This implies that forecasts of biodiversity change and dynamic conservation priorities need to be revised periodically leading to regular updating of spatial conservation priorities. Unless a realistic treatment of uncertainties is incorporated in the dynamic conservation planning process, the release of conservation areas will have risks that planners might not be willing to take. Our framework should thus be interpreted as a decision support tool rather than an expert tool for prescription of the areas in need to be released.

Several additional details can also be considered to increase realism in practical implementations of our framework. In our case study, we used Euclidean distances to define species' dispersal kernels. This is a simplistic implementation of a dispersal kernel because landscapes are heterogeneous and their impact on dispersal is species-specific. When species' ecologies are well understood and data are available, a more realistic permeability layer can be adopted for each of the species under analysis. Moreover, we defined costs as a function of the area covered by existing protected areas. In practice, conservation costs depend on several factors that could be accounted for if data were available (Carwardine *et al.* 2010; Armsworth *et al.* 2011; Shaw *et al.* 2012). For example, we did not consider the possibility of mitigating conservation costs by anticipating the value of areas before they became valuable, nor did we account for the income arising from the release of existing conservation areas. We also did not consider the possibility of dynamic land sale programmes in which land or easement transactions constitute sources of revenue for the protection of large amounts of areas that are necessary to safeguard species adaptation to climate change (Greene 2005). These land purchase schemes generate a complex 'economy' that may be analysed within the framework's cost task and may be considered for evaluation in terms of conservation benefits.

It may also be that the value of the conservation areas being considered is not exclusively associated with the species modelled. For example, in our case study, we used a small sample of terrestrial vertebrates and plants, and obviously they do not represent all biodiversity of interest. The extent to which a sample of biodiversity is a good surrogate for wholesale biodiversity constrains the usefulness of much quantitative spatial conservation prioritization exercises (Araújo, Densham & Williams 2004; Grantham *et al.* 2010; Sætersdal & Gjerde 2011). Additionally, most modelling of climate change impacts on species uses data and knowledge of the local species pool, but non-modelled species from other pools might colonize the regions of interest as a consequence of climate change. Such colonization might exacerbate local extinctions, but it might also lead to local increases in species richness (Sax & Gaines 2008). When one predicts species losses from climate change by modelling species in a given pool there is always a possibility that gains of species from other regions are being neglected (Thomas *et al.* 2012). Additionally, protected areas may also have been established for conserving broader and often intangible values (e.g., cultural, aesthetic, educational). When this is the case, release of areas because of species-specific targets might not be particularly welcomed (Chape *et al.* 2008).

Finally, although the description of the framework was focused on climate change, the dynamic factors causing changes in spatial conservation priorities can be diverse (Kareiva 2010). Again, the proposed framework is flexible and can be adapted to any type of quantifiable environmental or socio-economic change with effects on the distribution of conservation priorities in space and time.

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Supporting Information

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

Appendix S1. Formulation of the area prioritization problem.

Appendix S2. Setting 30-year maximum dispersal distances.

Fig. S1. Species dispersal kernel curves.

Fig. S2. Maps of planning-unit costs and habitat conversion in Iberian Peninsula and Balearic Islands.

Fig. S3. The individual species' persistences under an array of budgets for the dynamic and static spatial conservation prioritization strategies.

Fig. S4. The areas targeted for the optimization of species' persistences under a B1 future climate scenario using dynamic and static spatial conservation prioritization strategies.

Fig. S5. Agreement of the solutions and respective species-combined persistence obtained through various future climate scenarios, available budget for conservation areas acquisition, planning-unit costs, and species dispersal kernel curves.

Fig. S6. The areas selected to assist in the persistence of each species (forming 20 dispersal pathways per species) and the predicted climate suitability in Iberian Peninsula and Balearic Islands in different periods of time.

Table S1. Summary table of targeted areas and their timing of selection/release using the dynamic spatial conservation prioritization strategy.