Dynamic selection of dispersal pathways for species persistence under climate change

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Abstract — Ongoing climate change is already affecting distributions of many species. Future impacts of climate change are expected to be even greater. Conservation planning methodologies are usually based on the assumption that species distributions change relatively slowly unless they are directly affected by human activities, but this assumption is inappropriate under climate change. To address this problem we develop a model that, assuming a fixed budget limiting the selection of areas devoted to conservation, selects areas for each of different periods of time, and indicates how species disperse between selected areas on successive periods. These areas are termed dispersal pathways. Their effectiveness is assessed based on the performance to retain species suitable climates over time, and on the ability of species to disperse between the areas. The model identifies maximum effective dispersal pathways, limited to some given budget. We applied the model to nine Iberian species and considered four climate change and budgetary scenarios. Climate change scenarios assuming reductions of greenhouse gas emissions had relatively modest gains in species retention areas. But larger budgets for area selection translate in significantly better retention levels. Nevertheless, our model identified species that, regardless the high conservation investment attained with unlimited budget, have a very limited ability to disperse to climatically suitable areas. Connectivity enhancement and assisted colonization could be considered for such cases.

Keywords —Connectivity, Habitat suitability, Mathematical programming, Spatial conservation planning, Species' range shifts.

1 INTRODUCTION

There is an urgent need to assess the impact of climate change on biodiversity [1-2] in order to delineate measures to mitigate the expected negative consequences of such changes (e.g., species' range shifts and consequent loss of species representation within conservation areas) [3-5].

Implicit in assessing species range adjustments over time is the requirement that climatically suitable habitats are sufficiently connected through time and that species can disperse to remain in suitable environmental conditions. In such regard, a few

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modelling attempts have been proposed [6-8] to select a minimum number of areas assuring that a certain number of species populations persist as climate changes. These approaches have been especially dedicated to obtain solutions that achieve predefined conservation targets at minimum cost. A reversed approximation, where conservation targets are maximized for a given cost, can help quantifying the return-on-investment of conservation actions. Under such framework the following questions can be raised: How likely do targeted areas, whose selection is constrained by a given budget, retain species distributions within suitable climates under climate change? To what extent is a given budget sufficient to ensure retention of suitable climates across species distributions? Is species retention at all achievable?

We present a model to identify maximum effective dispersal pathways, subject to a given budget, that permits to addresses these questions. Dispersal pathways are collections of areas selected for each of different time periods, together with a indication on how species disperse between selected areas on successive periods. The model uses the species modelled climatic suitability of each area in different times in the future, and species specific dispersal ability to determine, given some budget that limits the selection of areas, dispersal pathways of maximum effectiveness. Effectiveness is assessed based on the performance of areas to retain species suitable climates over time, and on the ability of species to disperse between the areas. In order to

build future dispersal pathways preferentially from areas that are already being targeted for conservation, we penalize the selection of dispersal pathways away from existing protected areas. We thus assign a *cost* to every area, reflecting the unprotected surface area, and consider different budgets to limit area selection. Contrary to other approaches, that whenever an area is selected the corresponding cost is accounted regardless of its (previous and) later use, our model assesses, in each time period, if the conservation investments in the preceded periods are still required to achieve conservation targets and, if they are not, it deselects areas and transfers resources to other better valued areas.

Here we apply the proposed model in the study of retention levels of nine species with distinct climate tolerances in the Iberian Peninsula, using three global circulation models (CSIRO2, CGCM2 and HadCM3) averaged across two emission scenarios (e.g., A1FI, and B1). The model also explores two assumptions regarding the available budget for conservation (minimum required for non-null effectiveness level for every species, and unlimited budget).

2 METHODOLOGY

2.1 Data

We conducted the analysis for nine Iberian species (Table 1) listed as threatened by the European Habitats Directive [9] and/or World Conservation Union [10]. Records of presence and absence of species on a UTM 50x50 km grid resolution were obtained from European atlases of vertebrates [11-13] and plants [14] (for more details on the data see Williams et al. [15] and Araújo et al. [5]).

Table 1. Studied species and their taxonomic, conservation and dispersal characteristics.

Species	Common name	Taxa	List[1]	Dispersal[2] (km)
Marsilea quadrifolia	Four Leaf Clover	Plant	HD	40
Herniaria lusitanica	Hairy rupturewort	Plant	HD	30
Dianthus cintranus	-	Plant	HD	30
Paeonia officinalis	Common Peony	Plant	HD	20
Pleurodeles waltl	Iberian ribbed newt	Amphibian	RLVS	5
Lacerta schreberi	Schreiber's lizard	Reptile	RLVS	20
Otis tarda	Great bustard	Bird	RLVS	60
Galemys pyrenaicus	Pyrenean Desman	Mammal	RLVS	30
Mustela lutreola	European Mink	Mammal	RLVS	40

[1] *RLVS – Red List of Vertebrate Species;* HD – *Habitats Directive*
[2] *The maximum distance a species disperse in 30 years (Dmax)*

We derived four different climate parameters from original monthly-average climate data recorded from 1961-1991 (refereed to as 1990) and mapped at a 10' grid cell resolution. The variables were chosen to reflect major drivers of species distributions and include mean temperature of the coldest month, mean annual summed precipitation, mean annual growing degree days and a moisture index. We obtained future projections for the same variables using three global circulation models (CSIRO2, CGCM2 and HadCM3) for the periods of 1991-2020 (referred to as 2020), 2021-2050 (2050), and 2051-2080 (2080), and averaged results across two emission scenarios: A1FI and B1 [16: 167].

An ensemble forecasting strategy [17] was applied to combine projections from the different bioclimatic models and global circulation models. The climatic suitability, $S(u,sp,t)$, of each grid cell u for each species, sp, was obtained from bioclimatic suitability projections into four time periods, $t \in \{1990,2020,2050,2080\}$, at the resolution of the climate data. To avoid predicting species occurrences in the baseline period (1990) in grid cells where the species were not recorded, we converted all downscaled non-zero climate suitability scores to zero if they coincided with a grid cell where the species has not been recorded.

In order to focus the identification of suitable pathways for species dispersal in areas that are not directly exposed to anthropogenic threats, we used the human footprint index [18] as a measure of human pressure. "Footprint" values range from 0 to 100. Higher values correspond to greater levels of pressure. Here, we assumed that grid cells with a "footprint" above 50 would be unsuitable for the establishment of dispersal pathways for species.

A digital map of Iberian Peninsula protected areas was prepared from the World Database on Protected Areas [19]. We selected protected areas under the I-VI IUCN management categories and recorded the proportion of each grid cell covered by protected areas. For a more detailed description of the data and the modelling procedures see Araújo et al. [5].

In order to encourage the selection dispersal pathways within existing protected areas a cost value, $C(u,t)$, was assigned to each grid cell u and time t corresponding to the fraction of the grid cell area not covered by protected areas. Thus, if a grid cell is totally within protected areas, $C(u,t)=0$, for all time periods t.

We assumed for every species a maximum dispersal distance in each time period (Table 1), thus excluding the possibility for long-distance dispersal events. Since the time periods that were considered are of fixed length (30 years), we denote the maximum dispersal distance of species sp simply by $Dmax(sp)$ (without referring to t). For distances shorter than the maximum dispersal distance, we considered that the species ability to disperse from grid cell u to v, $D(u,v,sp)$, is a function of the Euclidean distance between u and v, $dist(u,v)$:

$$D(u,v,sp) = \begin{cases} \exp(-\alpha.dist(u,v)) & \text{if } dist(u,v) \leq Dmax(sp) \\ 0 & \text{if } dist(u,v) > Dmax(sp) \end{cases} \quad (1)$$

We chose α values so that the decay rate of dispersal ability decreases as *Dmax* gets larger.

2.2 The model

We term dispersal pathway any ordered chain of four grid cells $P=(u,v,w,z)$ that links grid cell *u* in 1990 to grid cell *z* in 2080, passing by grid cells *v* and *w* in 2020 and 2050, respectively. The effectiveness of dispersal pathways in retaining species, depends on the grid cells' climatic suitability and on the species' ability to move between the grid cells in a given time interval. To measure effectiveness we propose a species retention index for pathway *P*, which is defined as:

$$R(P,sp) = S(u,sp,1990) \times D(u,v,sp) \times S(v,sp,2020) \times ... \quad (2)$$
$$... \times D(w,z,sp) \times S(z,sp,2080)$$

which ranges between 0 and 1. The maximum retention, $R(P,sp)=1$ occurs when species *sp* remains in the same cell *u* during all periods and $S(u,sp,t)=1$ (for all time periods *t*). The minimum retention, $R(P,sp)=0$, occurs if a grid cell in the pathway is unsuitable for the species $S(u,sp,t)=0$, or if the distance between some pair of consecutive grid cells in pathway *P* exceeds the dispersal capacity of the species, *Dmax(sp)* .

Two or more dispersal pathways are said to non-overlap (in the same time period) when the grid cells used in the same period are distinct. A solution is a collection of a given number, *k(sp)*, of non-overlapping dispersal pathways for each species *sp*. The cost of a solution is the sum of the costs of the grid cells used in each period. As we have defined the cost of a grid cell as the fraction not covered by protected areas, the cost of a solution surrogates the amount of allocated resources outside existing protected areas network, counted only during the periods that they are used. The efficiency of a solution increases as more grid cells are used for multiple pathways. Since the pathways required for the same species are non-overlapping, efficient solutions tend to include grid cells for several species during the same time periods.

A solution is feasible if its cost does not exceed a given budget. Our model seeks to find a feasible solution that maximizes the sum of the retention indices across dispersal pathways. Note that optimal solutions for large budgets are likely to be less constrained since a large budget decreases the need for finding sets of pathways that overlap for different species. If there is no budget constraint,, an optimal solution can be obtained by maximizing the sum of the retention capabilities of the *k(sp)* dispersal pathways for each species *sp*, independently. Optimal solutions retrieve, for a given budget, the best retention opportunities for each species, regarding the number of pathways required for the species. Pathways with low retention values represent areas where species persistence through time is unlikely. Pathways with high retention values represent areas where species persistence under climate change is more likely.

We designed a mixed integer linear programming formulation for the above model, which fits in the multi-commodity flow setting [20: 649] devised by Philips et al. [7] for the problem, initially proposed by Williams et al. [6], of finding efficient sets of dispersal pathways for species under climate change. In our model, we define the sum of the retentions indices of the pathways as the objective to be maximized, and we treat efficiency as a constraint bounded by a given budget. In our approach efficiency is evaluated differently than by Philips et al. [7]. While these authors assume that once an area is selected in some time period, its cost is added even if the area is not used in all time periods, our model enables deselecting areas selected in previous time periods, only incorporating costs during the periods they are used. Saved costs from area deselecting are then applied in better-valued areas.

We used CPLEX 11.0 to run the model with the chosen nine species. The climatic suitability of species, $S(u,sp,t)$, were obtained from the distribution projections under the A1FI and B1 scenarios. We required $k(sp)=10$ dispersal pathways for each species and. for each climatic scenario we considered two alternative budgets: (i) minimum budget, i.e., letting the budget to be equal to the minimum value that guarantees the selection of $k(sp)=10$ non-zero retention pathways for each species *sp*; and (ii) unlimited budget, i.e., no budget constraint.

3 RESULTS

The model generates a sequence of areas to acquire (and release) across time that maximizes species retention for a given budget (Fig. 1). Solutions produced for the different emission scenarios overlap extensively (see overlap numbers in Table 2) but, augmenting the budget from the minimum (i.e., only assuring the selection of 10 non-zero retention dispersal pathways per species) to unlimited budget, causes more areas selected, especially along the western regions of Iberian Peninsula (Fig. 1). Indeed, solutions obtained with no budgetary limitations presented twice the number of grid cells when compared with the minimum budget approach. Under this latter scenario the turnover of selected/deselected grid cells is higher and it decreases with time, as the number of selected grid cells (Table 2).
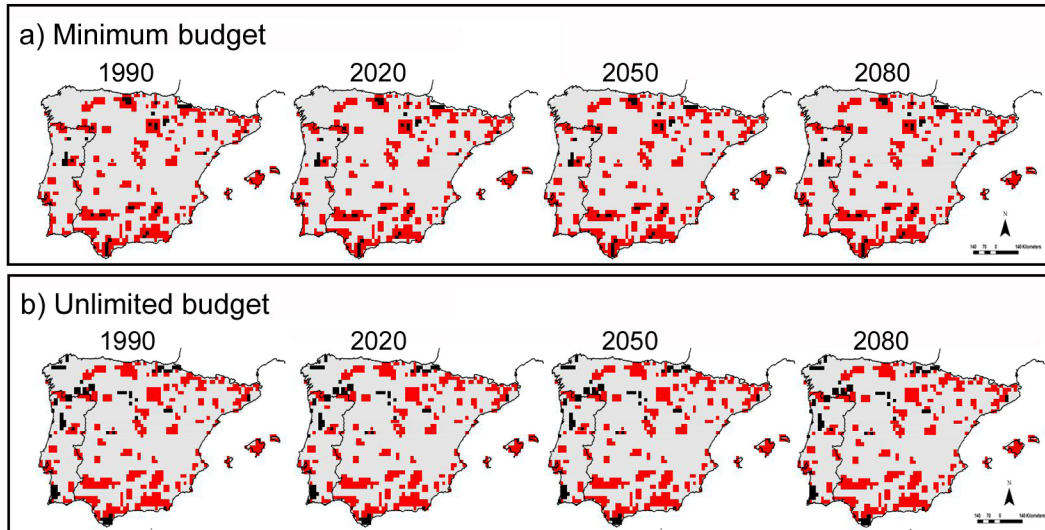
Fig. 1. The selected dispersal pathways (black grid cells) for the retention of nine species in the Iberian Peninsula, under the B1 climate scenario, using **a)** the minimum feasible budget and **b)** unlimited budget. Red grid cells (including more than 1% protected areas coverage) are favored regions for the selection of pathways.

Solutions obtained with no budgetary limitations present twice the number of grid cells when compared with the minimum budget approach. Under the former scenario there are few deselected grid cells across all time periods and the number of selected grid cells maintain constant. Under the latter scenario the number of deselected grid cells is higher while decreasing with time, like the number of selected grid cells (Table 2).

Table 2. Number of selected (Sel) and deselected (Desel) grid cells in each time period under two climate scenarios (A1FI and B1). In 1990, the number of deselected grid cells with more than 1% protected area coverage is indicated parenthetically. The spatial agreement of A1FI and B1 solutions is evaluated by the number of grid cells entering both solutions (Overlap).

	1990		2020		2050		2080
	Sel	**Desel**	**Sel**	**Desel**	**Sel**	**Desel**	**Sel**
Minimum budget							
A1FI	46	17(5)	44	8	41	2	39
B1	45	17(5)	43	8	40	2	38
Overlap	45		43		40		37
Unlimited budget							
A1FI	81	0(0)	81	2	81	2	81
B1	80	1(0)	80	3	80	0	80
Overlap	69		69		67		65

Although solutions produced under A1FI and B1, using the same budget, are similar in size, average retention success of dispersal pathways for the B1 scenario is higher for all nine species (Fig. 2). Nonetheless, the differences between the two scenarios are less marked when using the minimum budget. For each species, retention indices of the 10 dispersal pathways show important variability, especially under the minimum budget.

Changes in retention are mostly determined from budget availability. The average retention success of pathways increases markedly from minimum to unlimited budget. Major increments are expected for *Lacerta schreberi* (*c.* 22 times higher) and *Mustela lutreola* (*c.* 21 times higher), while *Herniaria lusitanica* and *Pleurodeles waltl*, are less favoured (*c.* 3 times higher) (Fig. 2). However, even with no budgetary limitations, *Marsilea quadrifolia*, and *Mustela lutreola* appear not to be able to track the expected climatic shifts, as their retention indices are close to zero.
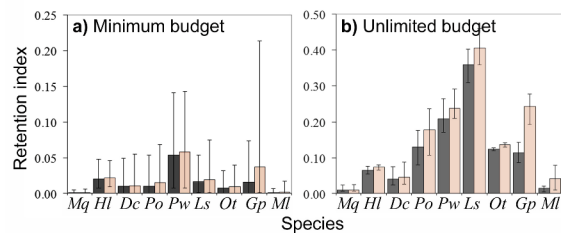

Fig. 2. Average retention of the 10 temporal corridors obtained with the **a)** minimum feasible budget and **b)** with unlimited budget for two climatic scenarios: A1FI (dark grey bars) and B1 (rose bars). Whiskers mark maximum and minimum retention values. *Mq: Marsilea quadrifolia; Hl: Herniaria lusitanica; Dc: Dianthus cintranus; Po: Paeonia officinalis; Pw: Pleurodeles waltl; Ls: Lacerta schreberi; Ot: Otis tarda; Gp: Galemys pyrenaicus; Ml: Mustela lutreola.*

Adopting the minimum budget approach restricts the potential success of species retention. By favouring grid cells predicted to be reasonable

suitable for several species simultaneously, climatic suitability of the selected grid cells is considerably lower than when using unbounded budget (Fig. 3). It should be mentioned that for the majority of species, the average grid cell's suitability with no budgetary constraint is not very different from what occurs if species could disperse freely between every two grid cells (i.e., $D(u,v,sp)=1$ and $Dmax(sp)=+\infty$). An exception is *Marsilea quadrifolia*, for which (the absolute values of) these differences are significantly increasing with time (Fig. 3). Under the B1 scenario, the climatic suitability for this species is predicted to increase (at least in some regions in Iberian Peninsula), but the species is not able to reach them.
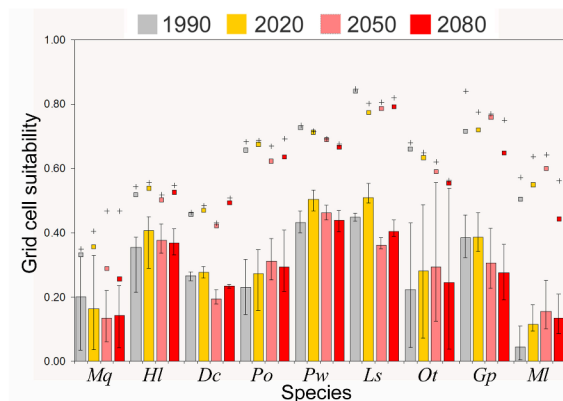

Fig. 3. Average suitability scores of the ten targeted grid cells to be used as dispersal pathways under the B1 climatic scenario, in different time periods. Bars refer to the minimum budget solution (whiskers mark the minimum and maximum scores). Filled squares refer to the unlimited budget solution and crossings refer to universal dispersal, $Dmax(sp)=+\infty$, with unlimited budget solution. *Mq: Marsilea quadrifolia; Hl: Herniaria lusitanica ; Dc: Dianthus cintranus; Po: Paeonia officinalis; Pw: Pleurodeles waltl; Ls: Lacerta schreberi; Ot: Otis tarda; Gp: Galemys pyrenaicus; Ml: Mustela lutreola.*

4 DISCUSSION

Spatial conservation planning when based simply on current needs of species risks wasting opportunities for achieving more effective and efficient conservation outcomes [21-22]. This is particularly true under climate change since species will need to move in and out of protected areas in order to track climate suitability. Here, we present a model that anticipates the identification of regions required to facilitate species' range shifts under climate change. The model uses assessments of changes of climatic suitability across space and time and makes assumptions of species' dispersal to determine the location of the candidate areas for the establishment of dispersal pathways. Final outcomes of the model are solutions to maximize species range retention in the future for a given budget. A dynamic mechanism of selection and deselection of areas for species dispersal is explored; the approach implements

principles of adaptive management and enables a more efficient allocation of scarce resources for conservation when priorities are bound to change through time and space.

In our implementation of the model, we found that albeit distinct emission scenarios are likely to inflict impacts of varying degrees on species potential distributions, the dispersal pathways required to enable adaptation of the nine species studied, have a significant degree of overlap between the A1FI and B1 scenarios. In other words, with climate changes of different magnitudes, the distribution of the different dispersal pathways does not differ markedly. However, as the two emission scenarios will impose different levels of local suitability, species retention within the selected pathways are likely to differ. For example, our study reports that the average corridor retention index increases c. 2% (for *Marsilea quadrifolia*) to c. 89% (*Mustela lutreola*) when comparing the more severe emission scenario (A1FI; lower values) with the less severe scenario (B1; higher values). Nonetheless, this tendency is veiled by the considerable within-species variation in the retention achieved by different pathways (ex. *Pleurodeles waltl* and *Galemys pyrenaicus* in Fig. 3a), denoting that the persistence of species is mostly dependent on a few critical pathways, to which prioritization should be given.

Our results also demonstrate that, more than reducing greenhouse gas emissions, it is the available budget for area acquisition the main factor determining conservation success (i.e., species retention). The available budget permits to select, in each time period, the areas most climatically suitable for each species. When budget is reduced the model is forced to select areas capable to support more species but with lower suitability. There are, however, species whose traits (e.g., low climatic tolerance, low dispersal rate) make them unequipped to follow the pace of climate change, even when dispersal pathways are selected with no budgetary constraints. This was the case of *Marsilea quadrifolia* and *Mustela lutreola* (Fig. 2), for which the targeted areas exhibit small retention expectancies. Under situations like these, three conservation mechanisms may rescue the species from regional extinction. First, averting habitat fragmentation and increasing landscape connectivity (e.g., decreasing the human footprint index in our case-study) could increase the chance that species tracks climate suitability as it changes [23-24]. Second, increasing carrying capacity and 'in situ' adaptation (e.g., increasing suitability values in our case-study) have been suggested to improve species resilience and recovery to change [25-26]. Third, using assisted colonization, a manipulative mechanism to physically relocate species in locations outside their existing or historical range that are predicted to be favourable for species

persistence [27-28]. In our analysis this option could be viable for species *Marsilea quadrifolia* and *Mustela lutreola* as suitable climate conditions are predicted to occur in some areas in Iberian Peninsula (Fig. 3). Whether this is worth doing depends on the magnitude of the potential gains for conservation and the required investment [29-30].

Additionally, the model presented here allows to plan (in advance) the areas to be selected as dispersal pathways making possible to avoid unnecessary conflicts with competing land-uses. This anticipative planning allows conservationists to engage society in the efforts to conserve biodiversity while preparing integrative management schemes to maintain the conservation value of the areas to be selected in the future. This requires new on-the-ground conservation instruments including the acquisition of development rights such as logging concessions, agri-environmental schemes and positive or negative incentives to landowners [31: 14, 32]. Conversely, there can be financial gains by trading areas whose conservation status reversed. These gains can be allocated to target better conservation-valued areas. If available, such kind of information can be easily incorporated in the here presented model [33-34].

Nonetheless, the use of coarse scale predictive data makes this kind of modelling prone to integrate uncertainties. Probabilistic data are the natural way to deal with uncertainties [35] and can enter directly into our model. Indeed, grid cell climatic suitability values could be directly substituted by probabilities of species occurrences (given the grid cell's climate) and dispersal abilities could be replaced by probabilities of a species to disperse to each grid cell in a given time interval. In such a case the retention index characterizing a pathway would inform on the probability of a species to persist across time if it occurs and disperses through that pathway.

Once identified the coarse-grain dispersal pathways with a model like the one herein proposed, finer-scale assessments based on much refined field data should be performed.

5 CONCLUSION

The combination of habitat suitability modelling with advanced reserve selection techniques allows the identification of dispersal pathways, which hold great promise for the adaptation of species under climate change. We have presented a spatially conservation prioritization approach that delineates cost-efficient dispersal pathways with the aim of maximizing retention of species ranges under a dynamic scenario of climate change. Unlike previous approaches, where conservation targets are met at minimum cost, our model operates maximizing conservation targets subject to some given cost. The model explicitly integrates an acquisition/ release procedure whereby the possibility of trading-off of areas selected in previous periods by new areas is allowed. This more realistically favors adaptive management schemes and the dynamic reallocation of the scarce resources into new areas as priorities change.

Our findings show that climate change mitigation efforts (reductions of greenhouse gas concentrations) have to be complemented with conservation planning strategies aimed at increasing the retention of species ranges in the landscapes. The approach proposed herein allows researchers and planners alike the identification of cost-effective dispersal pathways for species that enable species to track suitable climates as it changes. The approach is potentially useful to assist conservation prioritization schemes and guide policies aimed at promoting connectivity and assisted colonization under a changing climate.

REFERENCES

[1] Parmesan, C. and Yohe, G., A globally coherent fingerprint of climate change impacts across natural systems. *Nature.* 421(6918): p. 37-42, 2003.

[2] Thuiller, W., et al., Consequences of climate change on the tree of life in Europe. *Nature.* 470(7335): p. 531-534, 2011.

[3] Araújo, M.B., Cabeza, M., Thuiller, W., Hannah, L., and Williams, P.H., Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology.* 10(9): p. 1618-1626, 2004.

[4] Hannah, L., Midgley, G.F., and Millar, D., Climate change-integrated conservation strategies. *Global Ecology and Biogeography.* 11(6): p. 485-495, 2002.

[5] Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D., and Thuiller, W., Climate change threatens European conservation areas. *Ecology Letters,* 2011.

[6] Williams, P., et al., Planning for climate change: Identifying minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology.* 19(4): p. 1063-1074, 2005.

[7] Phillips, S., Williams, P., Midgley, G., and Aaron, A., Optimizing dispersal corridors for the Cape Proteaceae using network flow. *Ecological Applications.* 18: p. 1200-1211, 2008.

[8] Graham, C.H., VanDerWal, J., Phillips, S.J., Moritz, C., and Williams, S.E., Dynamic refugia and species persistence: tracking spatial shifts in habitat through time. *Ecography.* 33(6): p. 1062-1069, 2010.

[9] European Council, *Conservation of Natural Habitats and of Wild Fauna and Flora*, in *92/43/EEC,* 1992.

[10] IUCN, *IUCN Red List of Threatened Species. Version 2010.4.,* IUCN, http://www.iucnredlist.org, 2010.

[11] Gasc, J.P., et al., *Atlas of amphibians and reptiles in Europe.* Collection Patrimoines Naturels. Vol. 29. Paris:

Societas Europaea Herpetologica, Muséum National d'Histoire Naturelle & Service du Petrimone Naturel, 1997.

[12] Hagemeijer, E.J.M. and Blair, M.J., *The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance*. London: T & AD Poycer, 1997.

[13] Mitchell-Jones, A.J., et al., *The Atlas of European Mammals*. London: Academic Press, 1999.

[14] Jalas, J. and Suominen, J., *Atlas Florae Europaeae. Distribution of Vascular Plants in Europe*. Helsinki: The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, 1972-1996.

[15] Williams, P., et al., Endemism and important areas for representing European biodiversity: a preliminary exploration of atlas data for plants and terrestrial vertebrates. *Belgian Journal of Entomology*. 2: p. 21-46, 2000.

[16] Nakicenovic, N., et al., *Special Report on Emissions Scenarios: A Special Report of Working Group III of the Intergovernmental Panel on Climate Change*. Cambridge, U.K: Cambridge University Press, 2000.

[17] Araújo, M.B. and New, M., Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*. 22(1): p. 42-47, 2007.

[18] Sanderson, E.W., et al., The Human Footprint and the Last of the Wild. *BioScience*. 52(10): p. 891-904, 2002.

[19] IUCN and UNEP, *The World Database on Protected Areas (WDPA). UNEP-WCMC*, Cambridge, UK, http://www.wdpa.org, 2005.

[20] Ahuja, R.K., Magnanti, T.L., and Orlin, J.B., *Network Flows: Theory, Algorithms and Applications*. Upper Saddle River, New Jersey, USA: Prentice Hall, 1993.

[21] Drechsler, M., Eppink, F., and Wätzold, F., Does proactive biodiversity conservation save costs? *Biodiversity and Conservation*: p. 1-11, 2011.

[22] Spring, D.A., Cacho, O., Nally, R.M., and Sabbadin, R., Pre-emptive conservation versus "fire-fighting": A decision theoretic approach *Biological Conservation* 136(4): p. 531-540, 2007.

[23] Opdam, P. and Wascher, D., Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*. 117(3): p. 285-297, 2004.

[24] Spring, D., et al., Building a Regionally Connected Reserve Network in a Changing and Uncertain World. *Conservation Biology*. 24(3): p. 691-700, 2010.

[25] Sgrò, C.M., Lowe, A.J., and Hoffmann, A.A., Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications*. 4: p. 326-337, 2010.

[26] Jones, T.A. and Monaco, T.A., A role for assisted evolution in designing native plant materials for domesticated landscapes. *Frontiers in Ecology and the Environment*. 7(10): p. 541-547, 2009.

[27] Carroll, M.J., et al., Climate change and translocations: The potential to re-establish two regionally-extinct butterfly species in Britain. *Biological Conservation*. 142(10): p. 2114-2121, 2009.

[28] Loss, S.R., Terwilliger, L.A., and Peterson, A.C., Assisted colonization: Integrating conservation strategies in the face of climate change. *Biological Conservation*. 144(1): p. 92-100, 2011.

[29] McLachlan, J.S., Hellmann, J.J., and Schwartz, M.W., A Framework for debate of assisted migration in an era of climate change. *Conservation Biology*. 21(2): p. 297-302, 2007.

[30] Bottrill, M.C., et al., Is conservation triage just smart decision making? *Trends in Ecology & Evolution*. 23(12): p. 649-654, 2008.

[31] Araújo, M.B., *Protected areas and climate change in Europe. A discussion paper prepared for the 29th meeting of the Standing Committee, Convention on the Conservation of European Wildlife and Natural Habitats*, Coucil of Europe: Strasbourg, France, 2009.

[32] Garcia, R. and Araújo, M., Planejamento para a conservação em um clima em mudança. *Natureza & Conservação*. 8: p. 78-80, 2010. (*in Portuguese*)

[33] Mascia, M.B. and Pailler, S., Protected area downgrading, downsizing, and degazettement (PADDD) and its conservation implications. *Conservation Letters*. 4(1): p. 9-20, 2011.

[34] Fuller, R.A., et al., Replacing underperforming protected areas achieves better conservation outcomes. *Nature*. 466(7304): p. 365-367, 2010.

[35] Colyvan, M., Is probability the only coherent approach to uncertainty? *Risk Analysis*. 28(3): p. 645-652, 2008.