Climate Change and Spatial Conservation Planning

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13.1 Introduction

Spatial conservation planning methodologies have traditionally been implemented under the assumption that species distributions change relatively slowly, unless they are directly affected by human activities. However, over the past 100 years, Earth's climate has become warmer and precipitation regimes have changed. For example, from 1850–99 2001–05, global temperatures increased 0.76°C with warming in the past 50 years being nearly twice that for the last 100 years (IPCC 2007). Climate projections forecast even greater changes in the century to come, with impacts on biodiversity being expected to parallel changes in the climate (e.g. Thomas et al. 2004). Interactions of climate and land-use changes are only likely to compound the individual effects of climate change on biodiversity (e.g. Jetz et al. 2007; Pyke and Andelman 2007; Araújo et al. 2008). Environmental changes challenge the conventional approach to conservation planning, because they can alter the quantity, quality, and distribution of suitable areas for many species (e.g. Peters and Darling 1985; Hannah et al. 2002*b*). Some species will persist only if they can colonize new areas, although in some cases their dispersal abilities might be very limited and dependent on the existence of suitable 'stepping stones' between protected areas. In other cases, species might persist in areas where they can retain parts of their former ranges (i.e. 'range retention areas'); the question is whether such range retention areas and/or stepping stones for species dispersal have been captured by existing conservation areas and, if not, whether there are tools available for helping the identification of such critical areas for biodiversity conservation in a changing world.

In this chapter, I discuss some of the challenges to spatial conservation planning science to prevent or at least mitigate the impacts of climate change on biodiversity (Section 13.2). A focus on climate change is given, but the issues raised and the methodologies proposed could be extended and applied to any type of environmental change. I examine existing approaches for forecasting climate change impacts on species distributions (Section 13.3), and assess the relative merits of conventional spatial planning methodologies to identify conservation areas that will conserve species under changing climate conditions (Section 13.4.1). It is argued that progress in conservation planning requires a reassessment of conventional views on persistence, namely that local extinctions and colonizations are best characterized by meta-populations in a quasi-equilibrium state. A range of spatial conservation planning methodologies that could be implemented to help mitigate the impacts of climate change on species is also discussed (Section 13.4.2). Finally, a summary of the main issues discussed in the chapter is provided (Section 13.5). The need for a greater emphasis on interdisciplinary research in spatial conservation prioritization is also stressed.

13.2 Impacts of climate change on biodiversity

Climate change is already affecting the phenology and distributions of many terrestrial, freshwater, and marine species (e.g. Hughes 2000; Parmesan and Yohe 2003; Root et al. 2003) and projections for the twenty-first century predict even greater changes (e.g. Erasmus et al. 2002; Peterson et al. 2002; Thomas et al. 2004; Thuiller et al. 2005; Araújo et al. 2006; Huntley et al. 2008). This is not the first time species have been forced to adapt to climate changes. In the past, species have responded to climate changes by adapting, moving, or perishing. However, given the speed of current climate changes, adaptation by mutation and natural selection is likely to play a relatively minor role in the short term (but see Bradshaw and Holzapfel 2006). The capacity to colonize new areas is likely to be a more important mechanism of response to climate change, but it will vary across taxa and regions. Species with low vagility, low abundances, and low reproductive rates, specialized for given habitats or types of food are more likely to find it difficult to adapt to a changing world. This challenge will likely only be exaggerated in highly fragmented or degraded landscapes. Furthermore, the threats imposed by climate change do not act in isolation; they magnify the conventional threats associated with habitat degradation, pollution, poaching, and spread of alien invasive species. Spatial conservation planning faces this new challenge: the need for locating conservation areas and allocating resources for an unusually dynamic but also highly uncertain world.

13.3 Forecasting changes in species distributions

If spatial conservation planning is to anticipate climate change impacts on biodiversity and provide solutions to mitigate them, then the first step is to predict what impacts on species persistence are expected and where they are likely to occur. Predicting the future is obviously not trivial, but there are a wide range of approaches that can be used for modelling species responses to climate change. A familiar approach involves habitat suitability models (see also Chapter 6), also known as 'niche models, or 'bioclimatic envelopes' (though they may also include non-climatic habitat predictors), to project potential distributions of species under future climate scenarios (Pearson and Dawson 2003). These models utilize present-day distributions of species and combine them with climate variables to assess species–climate relationships and project distributions of species under future climate scenarios. Uncertainties in projections arising from projections of habitat suitability models have been extensively discussed in the literature (Chapters 6 and 11). They include ecological uncertainties arising from oversimplification of assumptions (e.g. Pearson and Dawson 2003; Guisan and Thuiller 2005), and algorithmic uncertainties associated with the use of different mathematical functions to fit the models (e.g. Heikkinen et al. 2006; Araújo and New 2007). However, because of their relative simplicity and availability of data for model building, habitat suitability models have been applied to large-scale, multi-taxa assessments of climate change impacts on biodiversity (e.g. Berry et al. 2002; Erasmus et al. 2002; Peterson et al. 2002; Thomas et al. 2004; Thuiller et al. 2005; Araújo et al. 2006; Huntley et al. 2008) and have had an impact well beyond the academic realm (e.g. IPCC 2007).

An alternative approach relies on process-based models. These models determine the mechanistic interactions between an organism's environment and its growth or fitness, usually based on theoretical inferences, experimental knowledge, or a combination of both. Examples of process-based models include dynamic vegetation models, commonly parameterized with physiological parameters generalized at the level of plant functional types (e.g. Woodward 1992), physiological models parameterized for individual species (e.g. Kearney and Porter 2004), metapopulation models (e.g. Hanski and Gaggiotti 2004), population viability analysis (e.g. Possingham and Davies 1995), and phenological models (Chuine et al. 2000). In contrast to habitat suitability models, process-based models usually begin with an analysis of the organism rather than its distribution. For example, in population viability analysis (Chapter 9), models often start with a characterization of mortality rates, fecundity rates, carrying capacity, and environmentally induced

variance. The output variables that are mapped onto geographical space are usually not probabilities of occurrence, or an index of habitat suitability, but instead a measure of growth or fitness (Kearney 2006). Exceptions include metapopulation models (Chapter 8) where a probability of patch occupancy is provided by the models. Because of their complexity, a limited number of process-based model applications have been used in a climate change context. In most cases, process-based models have been utilized to estimate biological responses to climate change at the biome or plant functional type level, and only recently have models been used to estimate the responses to climate change of a small number of species at a population level (Keith et al. 2008).

There are advantages and disadvantages with each one of these modelling approaches. Habitat suitability models are often regarded as a pragmatic option since they are relatively easy to parameterize and require species locality records that are widely available from museums, state-wide inventories, and distribution atlases (Chapter 6). These models provide precise forecasts within a limited reality, that is, when the circumstances in which models are calibrated are similar to the circumstances in which models are projected (e.g. Araújo et al. 2005; Araújo and Rahbek 2006). This is the case of forecasts made in the region where models are calibrated or forecasts made for time periods that are near to the period used for calibrating the models. Typically, process-based models are not based on statistical associations between variables and thus are expected to be more general than habitat suitability models (Guisan and Zimmermann 2000). In other words, they should be able to forecast patterns of species occurrences in circumstances that are very different from the situation used for model calibration. However, because process-based models require information that is typically unavailable for large numbers of species, the choice of parameters and the calibration of models are usually based on inferences from surrogate data or information obtained from limited samples. The solution is to generalize, for example, by grouping species into functional groups or assuming that populations are in a state of quasi-equilibrium. Because the effects of such generalizations are rarely tested, it is difficult

to assess whether forecasts from the more complex process-based models are better than forecasts from simpler habitat suitability models. In most circumstances, the choice of the modelling approach will be based on considerations of data availability, knowledge of the biology of the organisms involved, and last but not least the analytical background of the modeller.

13.4 Planning for species persistence

Spatial conservation prioritization tools seek to maximize the amount of species (or other biological attributes, such as habitats) that are represented in networks of areas for conservation (for conceptual clarification, see also Chapter 3). Typically, these methods use species distribution data from a particular time and rely on the premise that representing species within appropriately managed conservation areas will ensure their long-term persistence (e.g. Cabeza and Moilanen 2001). However, species ranges are naturally dynamic and conservation areas seeking to represent populations of particular species at a given place and time risk losing a proportion of their species or a proportion of the range of the species they are designated to conserve (Margules et al. 1994; Virolainen et al. 1999; Rodrigues et al. 2000; Araújo et al. 2002a), even when appropriate management is undertaken. The recognition that intrinsic species-population dynamics and extrinsic human-induced pressures affect the probability that species persist within conservation areas, has led to refinements of original quantitative conservation prioritization methods (Chapters 2 and 3). However, climate change poses new challenges for these methods. In the following section, the appropriateness of conventional spatial conservation prioritization approaches for ensuring persistence of species in the context of climate change is discussed (Section 13.4.1). Recommended changes to account for climate change in spatial conservation prioritization methodologies are provided (Section 13.4.2).

13.4.1 Planning for species persistence – conventional approaches

The challenge of climate change is an extension to the persistence problem in reserve selection (see

also Chapters 3, 8, 9, and 10), which addresses long-term dynamic challenges to species survival. A variety of methods have been developed to deal with different aspects of this problem, the most well-tested of which deals with habitat suitability and reserve connectivity (e.g. Nicholls and Margules 1993; Araújo and Williams 2000; Possingham et al. 2000; Williams and Araújo 2000; Moilanen and Cabeza 2002; Önal and Briers 2002; Cabeza 2003*a*; Cabeza et al. 2004*a*; Nicholson et al. 2006; Alagador and Cerdeira 2007; Haight and Travis 2008). A variety of software has been produced to implement these methods (for some examples,

see Chapters 14, and 15), which are based on two well-established principles. The first is that, all other things being equal, species are more likely to persist in suitable rather than unsuitable habitats (Figure 13.1, for an empirical demonstration of this statement see Araújo et al. 2002*a*). This generalization makes a number of assumptions regarding the relationship between local suitability, resource availability, carrying capacity, abundance and species' persistence and finds theoretical support in the law of population growth (Malthus 1798), environmental niche (Hutchinson 1957), and source–sink theories (Pulliam 1988).
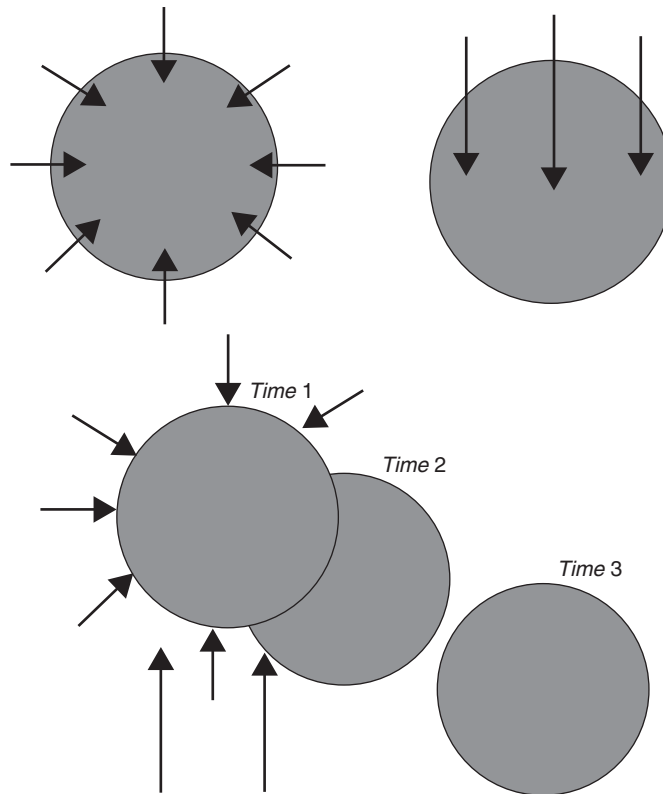

Figure 13.1 Models of range contraction: (*top left*) classic population model in which species are expected to contract from the periphery of their geographic or environmental range; (*top right*) contagious population model in which species are expected to contract from anywhere in geographic space and the threats spread like a disease, finally affecting the population that is most distant from the source of the contagion (by definition it is always a geographical periphery of the range); (*bottom*) population model under climate change in which apart from population dynamics and contagious contractions, there is a major displacement of suitable habitats for species. The arrows represent the direction of extinction forces.

The second principle is that large, compact, and better connected conservation areas are better than smaller and scattered ones (Diamond 1975*b*; Wilson and Willis 1975) (see also Chapters 3, 5, 8, 9, 14, and 15). This principle acknowledges the effects of area, isolation, and edge effects on the expected persistence of species within conservation areas and is supported from generalizations of island biogeography (MacArthur and Wilson 1963) and metapopulation theories (Levins 1969), as well as from empirical observations relating edge effects within conservation areas to the persistence of some species (Woodroffe and Ginsberg 2000).

Implementation of these principles is straightforward. Indeed, habitat suitability models (or process-based models, such as metapopulation models described in Chapter 8 or population viability models discussed in Chapter 9) can be easily combined with clustering methodologies to identify conservation areas that are both compact and located in areas of high habitat suitability for species (e.g. Cabeza et al. 2004*a*). However, there are at least two potential problems with the underlying assumptions of these models. The first is that reserve-connectivity might not be as general a rule for persistence as expected (for an extended discussion, see Shafer 2001). For example, increased distance between conservation areas might act as a safeguard against catastrophic or contagious degradation forces. The second is that the geographical distribution of threats may render the assumptions of high persistence probability in areas of high habitat suitability incorrect. Empirical observations of geographic range collapse for a broad range of taxonomic groups and regions have indeed shown that in the long term, peripheral and isolated populations can persist longer than populations at the core of their range (Lomolino and Channell 1995; Channell and Lomolino 2000). This is because threats are often spatially autocorrelated (e.g. McCarthy and Lindenmayer 2000), and extinction forces may progress contagiously, like a disease, across geographic space. When this is the case, regardless of where the contagious threat begins, the last place affected will be the region most isolated from the original source of the threat and this should always be along a range edge (Figure 13.1).

Given enough knowledge of the factors affecting the long-term persistence of species in a given region, it should be possible to integrate them into spatial conservation planning methodologies in a sequential way. Sequential approaches allow factors of different currencies and measurement scales to be combined, thus avoiding the combination of incompatible or non-interconvertible factors (also known as 'apples and oranges' problem, e.g. Williams and Araújo 2002). This procedure is preferred over the traditional combinatorial approaches (e.g. Goldsmith 1975; Anselin et al. 1989; Benayas and Montaña 2003), because assumptions are not required about the quantitative function linking factors, although the sequence with which factors are combined imposes an order of precedence that may be difficult to justify (Williams and Araújo 2002). Araújo et al. (2002*b*) proposes a sequential approach to integrate information on habitat suitability with extrinsic threats arising from human activities (Figure 13.2), but the principle is general and could be adapted to address a variety of conservation problems. Note that the term 'sequential' – used here to define a stepwise combination of factors that are relevant for a given conservation decision – has also been used to define a stepwise designation of conservation areas (e.g. Moilanen and Cabeza 2007).

The inclusion of suitability- and connectivity-based approaches into spatial conservation planning (see also Chapters 3, 4, 5, and 15) has been shown to improve the short-term persistence of species in theoretical reserve networks (e.g. Araújo et al. 2002*a*; Moilanen and Cabeza 2002; Cabeza and Moilanen 2003). The same should apply to real-world situations when species persistence is regulated by population dynamics that are in a state of quasi-equilibrium (such as that expected in metapopulations); or when persistence is affected by extrinsic human-induced threats that are explicitly accounted for in the conservation planning process (e.g. Williams et al. 2003; Rondinini and Boitani 2007; Strange et al. 2007). However, when climate change causes species ranges to shift away from their current locations (Figure 13.1), existing conservation areas may lose species in the mid to long term (e.g. Burns et al. 2003; Tellez-Valdes and DiVila-Aranda 2003; Lemieux and Scott 2005; Hannah et al. 2007).

The ability of familiar spatial conservation planning approaches to represent future-potential
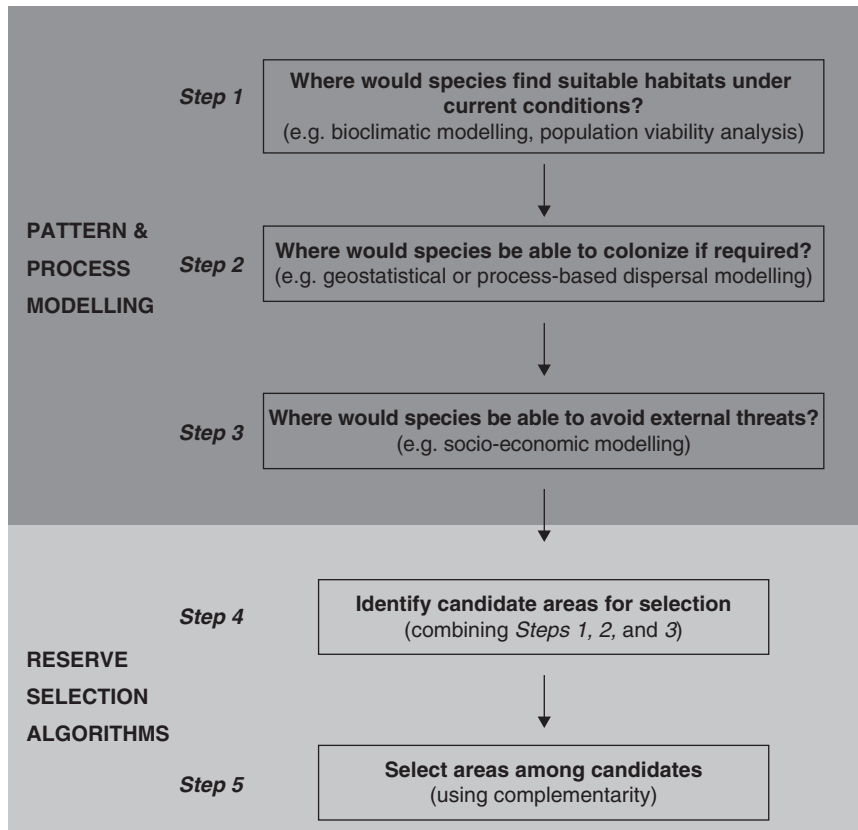
Figure 13.2 A generic approach for integrating persistence into conventional spatial conservation planning.

Note: Five stages are included, three of which fall in the realm of pattern and process-based modelling whereas the remaining two stages fall in the realm of spatial conservation prioritization.

distributions under climate change was tested using 1,200 European plant species (Araújo et al. 2004*a*). The tested approaches included: (*a*) a simple complementarity-based algorithm aimed at maximizing representation of species in conservation area networks using presence–absence data (Margules et al. 1988); (*b*) a complementarity-based algorithm aimed at maximizing representation of species but ensuring that conservation areas were clustered and as circular as possible (Possingham et al. 2000); (*c*) a complementarity-based algorithm aimed at maximizing representation of species but ensuring that selected conservation areas occurred in areas of high habitat suitability for each species (Araújo and Williams 2000). Under climate change,

all conservation areas were expected to lose species over a 50-year period, but clustered conservation areas lost more species than any other conservation areas scenario and more than expected by chance ($P < .05$). In contrast, conservation areas selected in high-quality habitat for each species lost fewer species than conservation areas selected by any other method (Table 13.1). Uncertainties arising from the choice of the dispersal scenario were less important than uncertainties associated with the choice of the conservation-areas selection technique.

What can we learn from these results? One important lesson is that arbitrary clustering of conservation areas may not always increase the probability of species persistence when climate change is the

Table 13.1 Representation of European plant species, in a baseline (1961–90) and future scenario (2021–50), in three hypothetical reserve networks and randomly generated sets of conservation areas. Two dispersal scenarios are considered between the baseline and future scenarios: no dispersal (species are not able to colonize new areas as they become suitable) and unlimited dispersal (species are able to colonize all new areas as they become suitable)

	Present		**Future**		Δ**dispersal**
Method (315 areas)		No dispersal	Unlimited dispersal		
Presence	100	92.92	93.94		1.02
Presence clustered	100	88.88	92.15		3.27
Presence threshold	100	93.45	94.47		1.02
Δ_{method}	–	4.57	2.32		–
Random*	99.33 (99.75)	89.02 (90.44)	92.88 (93.58)		

*Mean (representation value at $P < .05$, after 1,000 simulations).

Note: Variability in the results is calculated through a simple delta statistic (Δ = max representation–min representation).

Source: Modified from Araújo et al. (2004*a*).

main threatening process. There might be scale dependencies in regional patterns of species persistence that were overlooked in this study (50 km grid cells were used), but these results are not entirely surprising. The rationale for choosing single large versus several small reserves (see SLOSS debate in Chapter 8) is that metapopulations are the framework that best characterizes the dynamics of local populations, that is, local extinctions are expected to be 'rescued' by colonization from neighbouring populations. In a simple 'mainland–island' metapopulation model (Levins 1968), recolonization is assumed to be equally likely from one patch to any other, whereas in 'source–sink' models (Pulliam 1988) colonization is expected to be more likely from high-quality (source) to a poor-quality (sink) habitats. However, with climate change any of these assumptions might be unrealistic. In fact, major displacements of the quantity and quality of suitable habitats are expected with the possibility of disruption of standard metapopulation or source–sink dynamics. In particular, the assumption that colonizations and extinctions are in a quasi-equilibrium state is likely to be problematic.

Metapopulation theory predicts that a high number of extinctions in one generation should be followed by an increase of colonization events in subsequent generations, and vice versa. However, if extinctions are generated by shifting habitat suitabilities and populations track these changes by tracking habitats, then this feedback is broken and there is no reason to expect metapopulations to remain in equilibrium (Thomas and Hanski 2004). The exact process by which metapopulation dynamics ensures a process of colonization of suitable areas under climate change is still a matter of enquiry: Is it a transitional response with no clear disruption of a metapopulation structure? Is it an abrupt change forcing the metapopulation to disassemble and eventually assemble in a new location? A useful discussion of how metapopulation structure might change under climate change is provided by Opdam and Wascher (2004) and by Thomas and Hanski (2004). However, whatever the exact process by which populations adapt to climate change, it is clear that if the main driver of extinction is characterized by a directional displacement of habitats, then 'several small reserves' dispersed across the landscape might contribute to species persistence, for example, by providing stepping stones for dispersal (see also Figure 13.3 and the discussion in Section 13.3.2.1).

An additional source of concern is that adding rules for reserve clustering effectively trades off the shape of conservation areas with species representation. While representation-driven algorithms seek to maximize the number of species occurrences within reserve networks (i.e. once all species are represented in a set of conservation areas, the algorithm ensures that if more conservation areas are added they proportionally increase the number of occurrences of every species thus reducing overall
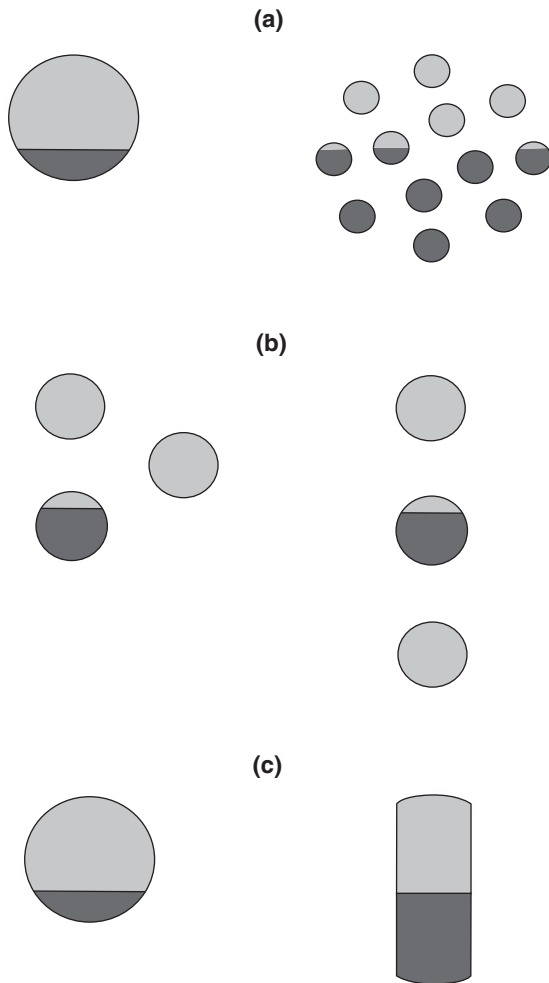
(a)

(b)

(c)

Figure 13.3 Geometric principles for the spatial arrangement of conservation areas. In each case (*a–c*) both the left and right designs have the same total area and conventional principles in reserve design suggest that conservation areas on the left are preferable to areas on the right. Light grey represents areas with current suitable climate, whereas dark grey represents areas with both current suitable climate and future suitable climate. The area of reserve remaining with suitable climate space in the future can be maximized by adopting several small reserves as opposed to a single large reserve (*a*) arranging disjunctive reserves linearly (*b*) or elongating reserves (*c*) in anticipation of shifting suitable climate space.

Source: Modified from Pearson and Dawson (2005).

extinction risk, see Chapters 3 and 4), reserve-clustering algorithms compromise potential increases in species representation by decreasing boundary length. The result is that reserve networks are more

circular and less scattered (thus being more robust to local stochastic extinctions), but they also tend to show a greater degree of compositional redundancy (i.e. some species may become over-represented while others may be under-represented). It follows that if one constrains an algorithm to cluster conservation areas around particular areas, one is likely to favour the conservation of geographically biased samples of species and habitats thus reducing the ability of species to adapt to changing environments (e.g. Pyke and Fischer 2005).

13.4.2 Planning for species persistence – incorporating climate change

Three alternative strategies for incorporating climate change into conservation prioritization exist: rules of thumb; range-retention areas; and dynamic complementarity-based reserve selection.

13.4.2.1 Rules of Thumb

If information on species distributions does not exist and detailed climate projections are not available, could one still make useful inferences for spatial conservation prioritization? A potential approach is based on rules of thumb. Conventional rules of thumb for reserve design were proposed by Diamond (1975*b*) and Wilson and Willis (1975). As discussed in the previous section (Section 13.4.1), these rules are based on simple principles derived from equilibrium theories of island biogeography and metapopulation ecology. More specifically, it is assumed that: (*a*) a large reserve is better than several small ones because of reduced extinction rates; (*b*) reserves should not be fragmented, or be as close as possible to increase the likelihood of dispersal between reserves; and finally, (*c*) reserves should be as nearly circular as possible to minimize dispersal distances within a reserve (but also to minimize edge effects, see Woodroffe and Ginsberg 2000).

Opdam and Wascher (2004) proposed three components of a strategy designed to address the conservation challenges imposed by climate change. The first is to stabilize key areas. Ecosystems most vulnerable to the combined effects of climate change and fragmentation would be developed as a spatial network, including large conservation areas as well

as landscape regions with coverage of natural and semi-natural habitats. Such 'nodes' of conservation would lower the risk of regional extinction under extreme climate perturbations and serve as sources of regional recovery. The second component is to ensure that the landscape is permeable, helping to ensure species can disperse and thus adapt to changed climatic conditions. The final component is to ensure habitat heterogeneity within conservation areas. Increasing the spatial variation of habitat types in conservation areas could favour local adaptation to climate change by ensuring short dispersal distances to suitable habitat. The first and second components are a logical consequence of the application of conventional principles of metapopulation theory to conservation and are related with the reserve design principles proposed by Diamond (1975*b*) and Wilson and Willis (1975). In contrast, the final strategy is unrelated to conventional reserve design principles and relates to the concept of 'range retention areas', or climate refuges (e.g. Pitelka 1997; Hannah et al. 2002; Araújo et al. 2004*a*) and these are explored in more detail in Section 13.4.2.2.

In the absence of species-specific information, simple rules could be used to assist conservation planners to devise adequate strategies to mitigate impacts of climate change on species persistence. Naturally, these rules need to be implemented with caution because it is difficult to account, with simple rules of thumb, for synergistic effects between climate change and non-climate change related threatening processes. Indeed and in contrast with conventional rules of thumb for reserve design, it has been noted by Pearson and Dawson (2005) that when there is a systematic displacement of habitats (e.g. northwards in the northern hemisphere, southwards in the southern hemisphere, and upwards in mountains), it is expected that sets of smaller conservation areas that are more distant might be more useful for species adaptation than a larger conservation area that covers a more restricted climatic gradient (Figure 13.3*a*). It might also be expected that elongated areas or conservation areas that follow given climatic gradients might provide the necessary stepping stones to allow species to track displacing habitats (Figure 13.3*b, c*). Furthermore, species are expected to respond to climate changes

in a complex, non-linear, and probably individualistic fashion (e.g. Huntley 1995). In order to account for individualistic behaviour of species, approaches should be employed that account for species-specific responses or that at least investigate species responses to climate change based on the expected responses of broad functional types (e.g. Thuiller et al. 2006).

13.4.2.2 Range Retention Areas

In the past, some regions have acted as Noah's arks of the world's biodiversity. In these places, species were able to persist for long periods of time despite the massive climate changes, as well as other environmental changes, that took place across the planet. Two kinds of climatic refugia, or, more generally, 'range retention areas' can be described: stationary refugia, where species were able to survive in regions that escaped the more dramatic climate extremes; and displaced refugia, where species were able to find suitable habitats after they had been displaced by climate changes from their original location (Newton 2003). Some patches of lowland tropical forest, large temperate forests in eastern Asia, steppe-tundra in the eastern parts of the Beringian region, sub-tropical laurel forests in oceanic islands remained relatively stable climatically and include some of the most well-known stationary refugia. In contrast, displaced refugia can be found in mountain ranges, deep valleys, and other areas with steep climate gradients that were able to maintain certain types of climate (cooler in warm periods and warmer in cold periods) that became regionally restricted.

Range retention areas have geographical properties that make them predictable from high resolution climate and digital elevation models. Recent attempts to extract biologically meaningful indicators from manipulation of climate variables hold much promise with regards to the identification of both past and future refugia for species diversity (e.g. Ohlemuller et al. 2006; Williams and Jackson 2007; Williams et al. 2007). Additionally, habitat suitability models can be used to predict distributions of both past (e.g. Waltari et al. 2007; Nogués-Bravo et al. 2008; Pearman et al. 2008) and future range retention areas (e.g. Araújo et al. 2004*a*). Given that dispersal is a risky strategy for species, conserving

range retention areas should be one of the first priorities for spatial conservation planning under climate change. These areas do not provide a sufficient template for conservation, but they could act as conservation 'nodes' which could then be linked with other important areas for conservation via the establishment of corridors or stepping stones.

13.4.2.3 Dynamic Complementarity-based Reserve Selection

The approaches discussed in the previous sections (rules of thumb and range retention areas) can be useful for locating important areas for biodiversity conservation under climate change, especially when no species data are available. Despite the potential usefulness of these two approaches in real-world conservation planning, they do not allow the kinds of optimization procedures that constitute the bulk of modern spatial conservation prioritization approaches. In other words, such procedures do not help answer questions, such as: How much is enough? Or, what is the best possible return for a given investment? Furthermore, despite the general interest in the conservation of ecosystem goods and services (for a debate, see McCauley 2006; Reid et al. 2006), conservation policy still uses species as the most common unit of conservation value (e.g. Caughley and Gunn 1996), and there is evidence that species have, by and large, responded to past climate changes individualistically (e.g. Graham and Grimm 1990). So, any conservation planning methodology that seeks to provide robust protocols for mitigating climate change impacts on biodiversity should include species-specific analyses of their expected responses to changes.

A general framework for integrating spatial prioritization procedures that mitigate the effects of climate change on species persistence is presented in Figure 13.4. Implementing such framework requires closer integration of classic spatial conservation prioritization research, with models predicting shifting habitat suitabilities, species dispersal, and species establishment and reproduction. The framework is general because it can be applied to any taxa and environment, and it does not imply the use of any particular model, nor does it imply that all of the first three steps are implemented. Depending on the availability of data and the resolution of the study,

one might start by implementing step 1 (e.g. macroecological studies with limited species-specific information), or step 1 and 2 (e.g. eco-regional studies where some species-specific information might allow general inferences about species dispersal), or step 1, 2, and 3 (e.g. local studies with a low number of species with well-known ecologies).

Williams et al. (2005c) were the first to formalize the climate change problem in reserve selection and provide a heuristic approach to maximize persistence of species under climate change, while seeking efficiency (achieving conservation goals at minimum cost) and flexibility (allow exploration of alternative reserve solutions that are equally effective in achieving a conservation goal). They developed an eco-regional case study for Proteaceae plants in the Cape floristic region in South Africa. The study included steps 1, 2, 4, and 5 of the framework (Figure 13.4) and the basic assumption was that long-term persistence of species would be achieved if at least $100\,m^2$ of predicted potential suitable climate conditions for every species would be contained in protected areas across a given 50-year period. To achieve this goal, multiple dispersal corridors, for each species, connecting areas with suitable climate conditions between periods were identified (Figure 13.5). Each dispersal corridor reflected the species' dispersal ability (dispersal distances assumed to be a maximum of one cell per time-slice for ant- and rodent-dispersed species, and a maximum of three cells per time-slice for wind-dispersed species) and minimized the total area requiring additional protection. Suitable habitat was identified by modelling the distributions of 280 plant species for the six 10-year time-slices between 2000 and 2050. Areas where species were expected to continue to occur in all of the six future time-slices, were treated as range retention areas (see also Section 13.4.2.2). These areas are expected to be the most reliable conservation areas under climate change, because dispersal is an uncertain and risky mechanism of adaptation of species to climate change. Where dispersal is required for adaptation, the approach developed by Williams et al. (2005c) identifies species needing urgent action and species for which there is little hope because dispersal is either unlikely or because the suitable climate space for the species is projected to disappear entirely. When dispersal is projected to
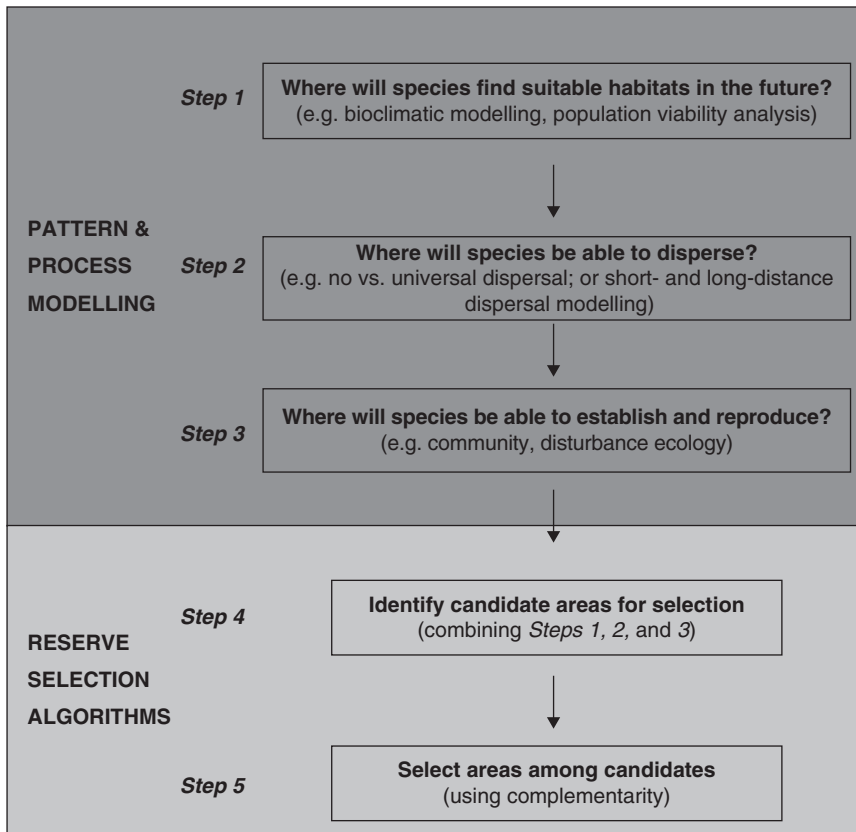
Figure 13.4 A generic approach for integrating persistence into conservation planning under climate change.

Note: This figure is a modification of Figure 13.2. Five stages are included, three of which fall in the realm of pattern and process-based modelling whereas the remaining two fall in the realm of spatial conservation prioritization.

be possible it might be facilitated by providing connectivity across the shortest corridors or chains of stepping stones over time.

This approach integrates projections of species range shift with conservation prioritization tools. Naturally, each step of the framework in Figure 13.4 can be improved in such a way as to increase realism of the assumptions and robustness of the methods used. In Williams et al. (2005*c*) projections of species range shifts were estimated with a single emission scenario, a single general circulation model, a single bioclimate model, and a single technique for transforming probabilities into presence absence. Each of these steps in the modelling adds a non-quantified, but potentially large, amount of uncertainty.

Ensemble forecasting enables simulations across the different steps of the modelling process, thus allowing an explicit treatment of uncertainties; this procedure is recommended when using projections of future climate impacts for decision planning (Araújo and New 2007). Furthermore, the technique for identifying dispersal chains and for optimizing selection of areas for conservation was based on a simple heuristic and there are more advanced methodologies to solve these problems. For example, a recent study Philips and colleagues replicated the study conducted by Williams et al. (2005*c*), but using an alternative approach for identifying the chains (using a technique called 'network flows') and using a mixed integer programme to select an
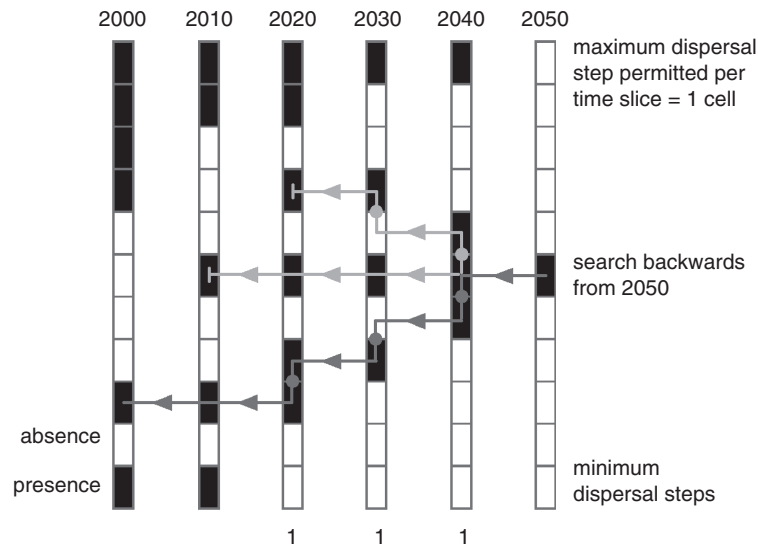
Figure 13.5 Procedure to identify dispersal corridors from modelled species' distribution data across different time-slices.

Note: Each vertical bar represents a one-dimensional map and each square represents a grid cell on the map. The different bars represent the successive time-slices. Black cells are modelled presences. The search for corridors begins at latest period because searching backwards is more efficient when range sizes are decreasing over time. To proceed to the next time-slice, there has to be a presence in the same grid cell or in a grid cell within one dispersal step (in this figure the maximum dispersal step allowed per time-slice is one grid cell). Only examples of two incomplete dispersal corridors and one complete corridor are shown. For selection of conservation areas only the complete corridor would be used.

Source: From Williams et al. (2005c).

optimal combination of chains that achieved the same conservation (Phillips et al. 2008). Use of these methods with the same data achieved an impressive reduction of one-third of the area required for conservation. This result is a reminder of the importance of interdisciplinary research in conservation planning and demonstrates that much improvement in conservation planning under climate change is still to be expected from the development of better quantitative tools for spatial prioritization.

13.5 Conclusion

Climate change presents an important challenge to conventional conservation planning, because species and their habitats are likely to shift away from their present locations. In this chapter, conventional approaches for incorporating species persistence into spatial conservation planning are reviewed. It is argued that climate change may render some familiar assumptions and conventional approaches

insufficient. For example, rules for reserve clustering are pertinent in situations of quasi-equilibrium between colonizations and extinctions in metapopulations. However, if extinctions are generated by shifting habitat suitabilities and species distributions are able to track these shifts, then there is no logical reason to expect metapopulations to exist in any kind of equilibrium. In some cases, a reversal of the conventional design principles, based on equilibrium biogeography and metapopulation theories, can occur. When this happens, conservation areas with geometric features that are traditionally viewed as sub-optimal can, effectively, maximize the conserved area that remains suitable in the future (Figure 13.3, Pearson and Dawson 2005). In other words, smaller conservation areas tracking pertinent climatic gradients might be, in some circumstances, preferable to large conservation areas occupying uniform climatic gradients.

This dichotomy between conventional conservation planning and the need for adequate

integration of climate change into conservation planning methodologies is not new. In fact, it reflects an old debate on the 'small' versus 'declining' population paradigms in conservation biology first coined by Caughley and Gunn (1996). Whereas the small population paradigm deals with the effects of low numbers of individuals in the long-term persistence of populations and metapopulations (a problem addressed with conventional conservation planning), the declining population paradigm deals with the causes of population decline before populations become small and vulnerable to demographic and environmental stochasticity (a problem addressed by climate change approaches). Ideally, the two approaches should be brought together, as they both offer a useful conceptual framework to address species persistence in conservation areas.

However, bringing together these two paradigms is difficult because rules of thumb offer all too simplistic solutions for complex problems, and because they tend to offer exclusive solutions. For example, the SLOSS debate is somehow spurious if we accept that both single large and several small reserves are necessary to conserve different components of biodiversity (e.g. mammals with large home ranges need single large reserves, whereas bryophytes are likely to benefit from several small). There might be value in shifting away from simple rules and developing pragmatic as well as theoretically robust solutions. As an alternative to simple rules of thumb, we propose a general framework for handling species persistence in conservation-area networks under climate change (Figure 13.4). Unlike previous rules of thumb, this framework does not provide a recipe for action. Rather, it provides a logical sequence of steps that are required for addressing a variety of factors affecting species persistence in a changing world. The framework is divided into two major components. Firstly, it asks where suitable habitats for species are more likely to occur in the future, what habitats are more likely to be colonized by species, and what habitats offer conditions for establishment and reproduction. Depending on the data

and resolution of the study, one might be forced to skip one or two of the framework's steps. Addressing these questions is within the realm of predictive modelling, which in turn draws its principles from theoretical and experimental ecology. The second part of the framework includes classic location allocation research or, more specifically, the development of suitable reserve selection algorithms. Greater integration between these two disciplines is required to formulate and solve problems of species persistence in conservation-area networks in a changing world.

When landscapes are highly fragmented and there are little options available for the establishment of new conservation areas, or stepping stones between areas, even the most robust spatial conservation planning methodologies might not find a cost-effective solution that enables adaptation of species to changing climate conditions. In such cases, it is important to acknowledge that conservation planning might need to consider radically different solutions, such as the artificial translocation of species and habitats (McLachlan et al. 2007). This possibility was not explored here, but it is important to acknowledge that in some cases artificial translocation might be a more effective and efficient policy than the creation of large-scale dispersal corridors.

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References

Alagador, D. and J. O. Cerdeira (2007). Designing spatially-explicit reserve networks in the presence of mandatory sites. Biological Conservation 137(2): 254-262.

Anselin, A., P. M. Meire and L. Anselin (1989). Multicriteria techniques in ecological evaluation: an example using the Analytical Hierarchy Process. Biological Conservation 49(3): 215-229.

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

Araújo, M. B. and M. New (2007). Ensemble forecasting of species distributions. Trends in Ecology and Evolution 22: 42-47

Araújo, M. B., D. Nogués-Bravo, I. Reginster, M. Rounsevell and R. J. Whittaker (2008). Exposure of European biodiversity to changes in human-induced pressures. Environmental Science & Policy 11(1): 38-45.

Araújo, M. B., R. G. Pearson, W. Thuiller and M. Erhard (2005). Validation of species-climate impact models under climate change. Global Change Biology 11: 1504-1513.

Araújo, M. B. and C. Rahbek (2006). How does climate change affect biodiversity? Science 313: 1396-1397.

Araújo, M. B., W. Thuiller and R. G. Pearson (2006). Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography 33: 1712-1728.

Araújo, M. B. and P. H. Williams (2000). Selecting areas for species persistence using occurrence data. Biological Conservation 96(3): 331-345.

Araújo, M. B., P. H. Williams and R. J. Fuller (2002). Dynamics of extinction and the selection of nature reserves. Proceedings of the Royal Society London Series B - Biological Sciences 269: 1971-1980.

Araújo, M. B., P. H. Williams and A. Turner (2002). A sequential approach to minimise threats within selected conservation areas. Biodiversity and Conservation 11: 1011-1024.

Benayas, J. M. R. and E. Montaña (2003). Identifying areas of high-value vertebrate diversity for strengthening conservation. Biological Conservation 114: 357-370.

Berry, P. M., T. E. Dawson, P. A. Harrison and R. G. Pearson (2002). Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. Global Ecology and Biogeography 11: 453-462.

Bradshaw, W. E. and C. M. Holzapfel (2006). Evolutionary Response to Rapid Climate Change. Science 312(5779): 1477-1478.

Burns, C. E., K. M. Johnston and O. J. Schmitz (2003). Global climate change and mammalian species diversity in U.S. national parks. PNAS 100(20): 11474-11477.

Cabeza, M. (2003). Habitat loss and connectivity of reserve networks in probability approaches to reserve design. Ecology Letters 6: 665-672.

Cabeza, M., M. B. Araújo, R. J. Wilson, C. D. Thomas, M. J. R. Cowley and A. Moilanen (2004). Combining probabilities of occurrence with spatial reserve design. Journal of Applied Ecology 41: 252-262.

Cabeza, M. and A. Moilanen (2001). Design of reserve networks and the persistence of biodiversity. Trends in Ecology and Evolution 16(5): 242-247.

Cabeza, M. and A. Moilanen (2003). Site-selection algorithms and habitat loss. Conservation Biology 17: 1-12.

Caughley, G. and A. Gunn (1996). Conservation Biology in theory and practice. Massachusetts, Blackwell Science.

Channell, R. and M. V. Lomolino (2000). Dynamic biogeography and conservation of endangered species. Nature 403: 84-86.

Chuine, I., G. Cambon and P. Comtois (2000). Scaling phenology from the local to the regional levels: advances from species-specific phenological models. Global Change Biology 6: 1-11.

Diamond, J. M. (1975). The island dilemma: lessons of modern biogeographic studies for the design of natural preserves. Biological Conservation 7: 129-146.

Erasmus, B. F. N., A. S. Van Jaarsweld, S. L. Chown, M. Kshatriya and K. J. Wessels (2002). Vulnerability of South African animal taxa to climate change. Global Change Biology 8: 679-693.

Goldsmith, F. B. (1975). The evaluation of ecological resources in the countryside for conservation purposes. Biological Conservation 8(2): 89-96.

Graham, R. W. and E. C. Grimm (1990). Effects of global climate change on the patterns of terrestrial biological communities. Trends in Ecology & Evolution 5(9): 289-292.

Guisan , A. and W. Thuiller (2005). Predicting species distribution: offering more than simple habitat models. Ecology Letters 8: 993-1009.

Guisan, A. and N. E. Zimmermann (2000). Predictive habitat distribution models in ecology. Ecological Modelling 135: 147-186.

Haight, R. G. and L. E. Travis (2008). Reserve design to maximize species persistence. Environmental Modeling & Assessment 13: 243-253.

Hannah, L., G. F. Midgley, S. Andelman, M. B. Araújo, G. Hughes, E. Martinez-Meyer, R. G. Pearson and P. H. Williams (2007). Protected area needs in a changing climate. Frontiers in Ecology and Environment 5: 131-138.

Hannah, L., G. F. Midgley, T. Lovejoy, W. J. Bond, M. Bush, J. C. Lovett, D. Scott and F. I. Woodward (2002). Conservation of biodiversity in a changing climate. Conservation Biology 16(1): 264-268.

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

Hanski, I. and O. E. Gaggiotti, Eds. (2004). Ecology, genetics, and evolution of metapopulations. San Diego, California, Elsevier Academic Press.

Heikkinen, R. K., M. Luoto, M. B. Araújo, R. Virkkala, W. Thuiller and M. T. Sykes (2006). Methods and uncertainties in bioclimatic modelling under climate change. Progress in Physical Geography 30: 751-777.

Hughes, L. (2000). Biological consequences of global warming: is the signal already apparent? Trends in Ecology and Evolution 15: 56-61.

Huntley, B. (1995). Plant species' response to climate change: implications for the conservation of European birds. IBIS 137: 127-138.

Huntley, B., Y. C. Collingham, S. G. Willis and R. E. Green (2008). Potential Impacts of Climatic Change on European Breeding Birds. PLoS ONE 3(1): e1439.

Hutchinson, G. E. (1957). Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22: 145-159.

IPCC, Ed. (2007). Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK, Cambridge University Press.

Jetz, W., D. S. Wilcove and A. P. Dobson (2007). Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds

PLoS Biology Vol. 5, (6): e157 doi:10.1371/journal.pbio.0050157.

Kearney, M. (2006). Habitat, environment and niche: what are we modelling? Oikos 115(1): 186-191.

Kearney, M. and W. P. Porter (2004). Mapping the fundamental niche: Physiology, climate, and the distribution of a nocturnal lizard. Ecology 85(11): 3119-3131.

Keith, D. A., H. R. Akçakaya, W. Thuiller, G. F. Midgley, R. G. Pearson, S. J. Phillips, H. M. Regan, M. B. Araújo and T. G. Rebelo (2008). Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models Biology Letters In press.

Lemieux, C. J. and D. J. Scott (2005). Climate change, biodiversity conservation and protected area planning in Canada. The Canadian Geographer/Le Géographe canadien 49(4): 384-397.

Levins, R. (1968). Evolution in changing environments: some theoretical explorations. Princeton, Princeton University Press.

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15: 237-240.

Lomolino, M. V. and R. Channell (1995). Splendid isolation: patterns of geographic range collapse in endangered mammals. Journal of Mammalogy 76: 335-347.

MacArthur, R. H. and E. O. Wilson (1963). An equilibrium theory of insular zoogeography. Evolution 17: 373-387.

Malthus, T. R. (1798). An essay on the principle of population, as it affects the future improvement of society with remarks on speculations of Mr. Godwin, Condorcet and other writers. London, J. Jonhson, in St. Paul's Church-yard.

Margules, C. R., A. O. Nicholls and R. L. Pressey (1988). Selecting networks of reserves to maximise biological diversity. Biological Conservation 43: 63-76.

Margules, C. R., A. O. Nicholls and M. B. Usher (1994). Apparent species turnover, probability of extinction and the selection of nature reserves: A case study of the Ingleborough limestone pavements. Conservation Biology 8(2): 398-409.

McCarthy, M. A. and D. B. Lindenmayer (2000). Spatially-correlated extinction in a metapopulation model of Leadbeater's possum. Biodiversity and Conservation 9: 47-63.

McCauley, D. J. (2006). Selling out on nature. Nature 443(7107): 27-28.

McLachlan, J. S., J. J. Hellmann and M. W. Schwartz (2007). A Framework for Debate of Assisted Migration in an Era of Climate Change. Conservation Biology 21(2): 297-302.

Moilanen, A. and M. Cabeza (2002). Single-species dynamic site selection. Ecological Applications 12: 913-926.

Moilanen, A. and M. Cabeza (2007). Accounting for habitat loss rates in sequential reserve selection: Simple methods for large problems. Biological Conservation 136(3): 470-482.

Newton, I. (2003). The speciation and biogeography of birds. London, Academic Press.

Nicholls, A. O. and C. R. Margules (1993). An upgraded reserve selection algorithm. Biological Conservation 64: 165-169.

Nicholson, E., M. I. Westphal, K. Frank, W. A. Rochester, R. L. Pressey, D. B. Lindenmayer and H. P. Possingham (2006). A new method for conservation planning for the persistence of multiple species. Ecology Letters 9(9): 1049-1060.

Nogués-Bravo, D., J. Rodriguez, J. Hortal, P. Batra and M. B. Araújo (2008). Climate Change, Humans, and the Extinction of the Woolly Mammoth. PLoS Biology 6(4): e79. doi:10.1371/journal.pbio.0060079.

Ohlemuller, R., E. S. Gritti, M. T. Sykes and C. D. Thomas (2006). Towards European climate risk surfaces: the extent and distribution of analogous and non-analogous climates 1931-2100. Global Ecology and Biogeography 15(4): 395-405.

Onal, H. and R. A. Briers (2002). Incorporating spatial criteria in optimum reserve network selection. Proceedings of the Royal Society London B 269: 2437-2411.

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

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

Pearman, P. B., C. F. Randin, O. Broennimann, P. Vittoz, W. O. v. d. Knaap, R. Engler, G. L. Lay, N. E. Zimmermann and A. Guisan (2008). Prediction of plant species distributions across six millennia. Ecology Letters 11(4): 357-369.

Pearson, R. G. and T. E. Dawson (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12: 361-371.

Pearson, R. G. and T. P. Dawson (2005). Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. Biological Conservation 123(3): 389-401.

Peters, R. L. and J. D. Darling (1985). The green-house effect and nature reserves. BioScience 35: 707.

Peterson, A. T., M. A. Ortega-Huerta, J. Bartley, V. Sanchez-Cordero, J. Soberon, R. H. Buddemeier and D. R. B. Stockwell (2002). Future projections for Mexican faunas under global climate change scenarios. Nature 416: 626-629.

Phillips, S. J., P. Williams, G. Midgley and A. Archer (2008). Optimizing dispersal corridors for the Cape Proteaceae using network flow. Ecological Applications In press.

Pitelka, F. (1997). Plant migration and climate change. American Scientist 85: 464-473.

Possingham, H. P., I. Ball and S. Andelman (2000). Mathematical methods for identifying representative reserve networks. Quantitative Methods for Conservation Biology. S. Ferson and M. Burgman. New York, Springer-Verlag: 291-305.

Possingham, H. P. and I. Davies (1995). Alex: a model for the viability analysis of spatially structured populations. Biological Conservation 73: 143-150.

Pulliam, H. R. (1988). Sources, sinks, and population regulation. The American Naturalist 132(5): 652-661.

Pyke, C. and S. Andelman (2007). Land use and land cover tools for climate adaptation. Climatic Change 80(3): 239-251.

Pyke, C. R. and D. T. Fischer (2005). Selection of bioclimatically representative biological reserve systems under climate change. Biological Conservation 121(3): 429-441.

Reid, W. V., H. A. Mooney, D. Capistrano, S. R. Carpenter, K. Chopra, A. Cropper, P. Dasgupta, R. Hassan, R. Leemans, R. M. May, P. Pingali, C. Samper, R. Scholes, R. T. Watson, A. H. Zakri and Z. Shidong (2006). Nature: the many benefits of ecosystem services. Nature 443(7113): 749-749.

Rodrigues, A. S., R. D. Gregory and K. J. Gaston (2000). Robustness of reserve selection procedures under temporal species turnover. Proceedings of the Royal Society London B 267: 49-55.

Rondinini, C. and L. Boitani (2007). Systematic Conservation Planning and the Cost of Tackling Conservation Conflicts with Large Carnivores in Italy. Conservation Biology 21(6): 1455-1462.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig and J. A. Pounds (2003). Fingerprints of global warming on wild animals and plants. Nature 421: 57-60.

Shafer, C. L. (2001). Inter-reserve distance. Biological Conservation 100(2): 215-227.

Strange, N., I. Theilade, S. Thea, A. Sloth and F. Helles (2007). Integration of species persistence, costs and conflicts: An evaluation of tree conservation strategies in Cambodia. Biological Conservation 137(2): 223-236.

Tellez-Valdes, O. and P. DiVila-Aranda (2003). Protected areas and climate change: a case study of the Cacti in the Tehuacan-Cuicatlan Biosphere Reserve, Mexico. Conservation Biology 17(3): 846-853.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. J. Miles, M. A. Ortega-Huerta, A. Townsend Peterson, O. Phillips and S. E. Williams (2004). Extinction risk from climate change. Nature 427: 145-148.

Thomas, C. D. and I. Hanski (2004). Metapopulation dynamics in changing environments: butterfly responses to habitat and climate change. Ecology, genetics, and evolution of metapopulations. I. Hanski and O. E. Gaggiotti. San Diego, California, Elsevier.

Thuiller, W., S. Lavorel, M. B. Araújo, M. T. Sykes and I. C. Prentice (2005). Climate change threats plant diversity in Europe. Proceedings of the National Academy of Sciences, USA 102: 8245-8250.

Thuiller, W., S. Lavorel, M. T. Sykes and M. B. Araujo (2006). Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. Diversity and Distributions 12(1): 49-60.

Virolainen, K. M., T. Virola, J. Suhonen, M. Kuitunen, A. Lammi and P. Siikamaki (1999). Selecting networks of nature reserves: methods do affect long-term outcome. Proceedings of the Royal Society London Series B - Biological Sciences 266: 1141-1146.

Waltari, E., R. J. Hijmans, A. T. Peterson, Ã. r. d. S. NyÃ¡ri, S. L. Perkins and R. P. Guralnick (2007). Locating Pleistocene Refugia: Comparing Phylogeographic and Ecological Niche Model Predictions. PLoS ONE 2(7): e563.

Williams, J. W. and S. T. Jackson (2007). Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment 5(9): 475-482.

Williams, J. W., S. T. Jackson and J. E. Kutzbacht (2007). Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences of the United States of America 104(14): 5738-5742.

Williams, P. H. and M. B. Araújo (2000). Using probability of persistence to identify important areas for biodiversity conservation. Proceedings of the Royal Society London Series B - Biological Sciences 267: 1959-1966.

Williams, P. H. and M. B. Araújo (2002). Apples, oranges, and probabilities: Integrating multiple factors into biodiversity conservation with consistency. Environmental Modeling and Assessment 7: 139-151.

Williams, P. H., L. Hannah, S. Andelman, G. F. Midgley, M. B. Araújo, G. Hughes, L. L. Manne, E. Martinez-Meyer and R. G. Pearson (2005). Planning for Climate Change: Identifying Minimum-Dispersal Corridors for the Cape Proteaceae. Conservation Biology 19: 1063-1074.

Williams, P. H., J. L. Moore, A. K. Toham, T. Brooks, H. Strand, J. A. D'Amico, M. Wisz, N. Burgess, A. Balmford and C. Rahbek (2003). Integrating biodiversity priorities with conflicting socio-economic values in the Guinean-Congolian forest region. Biodiversity and Conservation 12: 1297-1320.

Wilson, E. O. and E. O. Willis (1975). Applied biogeography. Ecology and Evolution of Communities. M. L. Cody and J. M. Diamond. Cambridge, USA, Belknap Press: 522-534.

Woodroffe, R. and J. Ginsberg (2000). Ranging behaviour and vulnerability to extinction in carnivores. Behaviour and Conservation. L. M. Gosling and W. J. Sutherland. Cambridge, Cambridge University Press. 2: 125-140.

Woodward, F. I. (1992). Predicting plant responses to global environmental change. New Phytologist 122: 239-251.