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Would climate change drive species out of reserves? An assessment of existing reserve-selection methods

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Abstract

Concern for climate change has not yet been integrated in protocols for reserve selection. However if climate changes as projected, there is a possibility that current reserve-selection methods might provide solutions that are inadequate to ensure species' long-term persistence within reserves. We assessed, for the first time, the ability of existing reserve-selection methods to secure species in a climate-change context. Six methods using a different combination of criteria (representation, suitability and reserve clustering) are compared. The assessment is carried out using European distributions of 1200 plant species and considering two extreme scenarios of response to climate change: no dispersal and universal dispersal. With our data, 6–11% of species modelled would be potentially lost from selected reserves in a 50-year period. Measured uncertainties varied in 6% being 1–3% attributed to dispersal assumptions and 2–5% to the choice of reserve-selection method. Suitability approaches to reserve selection performed best, while reserve clustering performed poorly. We also found that 5% of species modelled would lose their entire climatic envelope in the studied area; 2% of the species modelled would have nonoverlapping distributions; 93% of the species modelled would maintain varying levels of overlapping distributions. We conclude there are opportunities to minimize species' extinctions within reserves but new approaches are needed to account for impacts of climate change on species; especially for those projected to have temporally nonoverlapping distributions.

Keywords: bioclimatic modelling, climate change, complementarity, conservation planning, dispersal, distribution models, habitat suitability, persistence, probabilities of occurrence, reserve clustering, reserve selection

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Introduction

Quantitative reserve-selection methods seek to maximize the amount of biodiversity that can be represented in networks of areas for conservation (Margules & Pressey, 2000). Typically, these methods use species distribution data for particular time and rely on the

premise that representing species within appropriately managed reserves would ensure their long-term persistence (Cabeza & Moilanen, 2001). However, species ranges are naturally dynamic and reserves seeking to represent populations of particular species at a given place and time risk losing a proportion of their species (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 reserves led to various

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refinements of original quantitative reserve-selection methods. However, climate change poses a new challenge for these methods.

The challenge of climate change is an extension to the persistence problem in reserve selection, 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 deal with habitat suitability and reserve connectivity (Nicholls & Margules, 1993; Araújo & Williams, 2000; Possingham *et al.*, 2000; Williams & Araújo, 2000, 2002; Araújo *et al.*, 2002b; Briers, 2002; Onal & Briers, 2002; Cabeza, 2003; Cabeza *et al.*, 2004a). These methods 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 (Araújo & Williams, 2000); this generalization makes a series of assumptions on 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). The second is that large, compact and better connected reserves are better than smaller and scattered ones (Diamond, 1975); this idea acknowledges the effects of area, isolation and edge effects on the expected persistence of species within reserves and is supported from generalizations of island biogeography (MacArthur & Wilson, 1963) and metapopulation theories (Levins, 1969), as well as from empirical observations relating edge effects, within reserves, to persistence of wide-ranging species (e.g. Woodroffe & Ginsberg, 2000). Mixed approaches bringing suitability and reserve connectivity together have also been devised (Cabeza *et al.*, 2004a), but there is a concern that reserve connectivity might not be as general a rule for persistence as expected (Shaffer, 2001).

Even though existing suitability- and connectivity-based approaches have been shown to improve expected short-term persistence of species in theoretical reserve networks (Araújo *et al.*, 2002a; Moilanen & Cabeza, 2002; Cabeza & Moilanen, 2003), there is a concern that changes in climate conditions might cause species' ranges to move away from their current locations (e.g. Parmesan *et al.*, 1999; Thomas & Lennon, 1999; Hughes, 2000; Warren *et al.*, 2001; Parmesan & Yohe, 2003; Root *et al.*, 2003). In such cases there is a possibility that reserves selected with existing approaches might be inadequate to guarantee species' persistence in the long term (Peters & Darling, 1985; Cowling *et al.*, 1999; Araújo *et al.*, 2002a; Hannah *et al.*, 2002; Scott *et al.*, 2002). We test this possibility, for the first time, by measuring the performance of six familiar

reserve-selection techniques to represent future distributions of 1200 European plant species projected to shift their ranges as a consequence of a climate-change scenario for 2050. This analysis has important practical implications for how reserve systems should be designed in the future. It offers insight into possible improvements of reserve-selection methods to deal with climate change and the likely importance of such improvement, for one region.

Data and methods

Species and climate data

Original species data included records of occurrence for 1200 plant species (Jalas & Suominen, 1972–1996) digitized from the Atlas Florae Europaeae (AFE) by Lahti & Lampinen (1999). Only species with more than 25 occurrence records in the original data set were modelled. Species retained included all pteridophytes, a sample of spermatophytes comprising all gymnosperm families, and a sample of angiosperms (Salicales, Myricales, Junglandales, Fagales, Urticales, Proteales, Santales, Aristolochiales, Balanophorales, Polygonales, Centrospermae and Ranales). The grid used follows 50 km lines of the Universal Transverse Mercator (UTM) grid, except near the border of the 6° UTM zones and at coasts. The mapped area (2434 grid cells) included western, northern and southern Europe, but excluded most of the eastern European countries (except for the Baltic States), where recording effort was both less uniform and less intensive (for more details on data conversion, see Williams *et al.*, 2000).

Original climate data comprised five monthly time-step variables developed for the project Advanced Terrestrial Ecosystem Analysis and Modelling (ATEAM) at a 10' grid resolution (Mitchell *et al.*, 2004; <http://www.cru.uea.ac.uk/~timm/data/index-table.html>). The variables included temperature (°C), diurnal temperature range (°C), precipitation (mm), vapour pressure (hP), and cloud cover (%) for the 20th and 21st centuries (1901–2100). The climate data used in this paper consist of seven variables derived from the original ATEAM climate data set, and then resampled to the AFE 50 km grid system to match species data. These seven derived variables included mean annual temperature (°C), mean temperature of the coldest month per year (°C), mean annual precipitation sum (mm), mean annual winter precipitation sum (mm), mean annual summer precipitation sum (mm), mean annual growing degree days (>5°), mean ratio of annual actual evapotranspiration over annual potential evapotranspiration. The selected climate variables are regarded as determinants of physiological processes

limiting distributions of plant species (Bartlein *et al.*, 1986; Woodward, 1987; Prentice *et al.*, 1992). These variables were averaged over two 30 years periods: baseline climate data included the period of 1961–1990, while scenario data included the period of 2021–2050. As an example we used the HadCM3 General Circulation Model (GCM), under IPCC extreme A1FI SRES emission marker scenario. Under this scenario, atmospheric CO₂ should rise from 380 ppm in 2000 to 580 ppm in 2050. Mean annual temperatures in Europe are forecasted to increase from current 8.3 °C to 10.4 °C for 2021–2050.

Bioclimatic modelling

For each species, we predicted current and projected future probabilities of occurrence in the 50 km grid cells using generalized additive models (GAMs). We calibrated models for current conditions on a 70% random sample of the initial data and evaluated models on the remaining 30% of the data, using the κ statistic approach (Monserud & Leemans, 1992). Fitted models for each species were then used to project future potential distributions in response to a climate-change scenario. Models were run using S-Plus-based BIOMOD application (Thuiller, 2003). There are many uncertainties associated to projecting current and future distributions using standard bioclimatic modelling techniques. Some of these uncertainties have been discussed and addressed elsewhere (Pearson & Dawson, 2003; Thuiller, 2003; Segurado & Araújo, 2004;

Thuiller *et al.*, 2004) and although they are important we do not explore the issue any further here.

Reserve selection methods

In order to ensure comparability among reserve-selection methods, we selected reserve networks with an equal number of grid cells. This was done by first identifying the minimum n set of areas (here 315 grid cells) required to achieve a given conservation goal with the method requiring the largest amount of area (here method 5). We then found alternative reserve network solutions, by setting the remaining methods with more ambitious goals, reordering selected areas by increments of complementarity, and then selecting the top n (here 315) areas from the ordered list. Maximum-coverage solutions, where a particular conservation goal is maximized for a given area (Church *et al.*, 1996), can be approximated using these heuristics (Williams *et al.*, 2000). Overall, we compared six reserve-selection methods (Table 1): (1) *presence method*, using Margules *et al.* (1988) minimum-set algorithm coupled with additional redundancy checks (Williams *et al.*, 2000), (2) *presence clustered method* based on method 1, but using a function that minimizes a linear combination of reserve area and reserve boundary length (Possingham *et al.*, 2000; Cabeza *et al.*, 2004b), (3) *presence threshold method* with occurrence records filtered by n (here 0.85) rescaled probability of occurrence threshold (Araújo & Williams, 2000), so that only species locational records with high suitability scores for every species are

Table 1 Reserve selection approaches used for comparison

No.	Method	Goal	Input data	Method
1	Presence	Maximize species representation for a given area	Presence records	Margules <i>et al.</i> (1988) and Williams <i>et al.</i> (2000)
2	Presence clustered	Maximize species representation for a given areas, but minimizing reserve boundary length	Presence records	Possingham <i>et al.</i> (2000) and Cabeza <i>et al.</i> (2004b)
3	Presence threshold	Maximize species representation for a given area, but only within top of suitable habitats within every species ranges	Probabilities	Araújo & Williams (2000)
4	Goal gap	Maximize species probabilities of occurrence for a given area	Probabilities	Williams & Araújo (2000)
5	Goal gap clustered	Maximize species probabilities of occurrence for a given area and boundary length	Probabilities	Cabeza <i>et al.</i> (2004a)
6	Goal gap threshold	Maximize species probabilities of occurrence for a given area, but only within top suitable habitats within every species ranges	Probabilities	Araújo <i>et al.</i> (2002a) and Williams & Araújo (2002)

considered for selection, (4) *goal gap* that maximizes species probabilities of occurrence for a given area (Williams & Araújo, 2000, 2002), (5) *goal-gap clustered method* that aims at achieving a given probability target for all species while minimizing a linear combination of reserve area and reserve boundary length (Cabeza *et al.*, 2004a), and (6) *goal-gap threshold method* with probability records filtered by n (here 0.85) rescaled probability threshold (Araújo *et al.*, 2002a; Williams & Araújo, 2002). A *random solution* was also obtained by selecting a given number of areas at random 1000 times. The 5% upper tail of the random distribution was used as an estimate of whether observed set representation values obtained with other methods are greater than expected by chance ($P > 0.05$).

Because there were many fully flexible alternative solutions among presence methods we obtained nine additional solutions by breaking ties at random (they were previously broken by selecting areas among ties with the lowest grid-cell number). Flexibility occurs when multiple localities capture the same critical set of species, and thereby provides options for negotiation and establishing reserve networks (Williams *et al.*, 2003). We used all 10 flexible solutions to calculate mean species representation within reserves as well as standard deviations under future conditions. This allowed us to estimate stability of results, which is important when using surrogate approaches (i.e. using present conditions to conserve future conditions) in the face of multiple flexible solutions (for discussion see Hopkinson *et al.*, 2001). Multiple solutions were not obtained for goal-gap approaches because there are fewer ties to break when using data other than presence/absence (e.g. probabilities of occurrence, abundance). WORLDMAP software (Williams, 1999) was

used to implement methods 1, 3, 4, 6 and 7; methods 2 and 5 used a similar clustering algorithm as in MARXAN (Ball, 2000) and SITES (Andelman *et al.*, 1999), but with modifications to allow approximations to maximum-coverage solutions (Cabeza *et al.*, 2004a, b).

The performance of reserve-selection methods in securing species with climate change is assessed in the context of two extreme scenarios: no-dispersal; and universal dispersal (see also Sykes & Prentice, 1996; Peterson *et al.*, 2002). No-dispersal means that only areas that are modelled to be suitable both in the present and in the future will be occupied by the species in the future. Universal dispersal means that all areas with suitable conditions in the future will be occupied by the species. Although both scenarios are likely to be unrealistic (Pitelka, 1997), they summarize the range of uncertainties associated with species' varying dispersal, establishment and reproductive abilities. More realistic scenarios would require that both short- and long-distance dispersal were modelled, but there are still many uncertainties with these processes – especially with long-dispersal modelling (e.g. Higgins & Richardson, 1999) – that fall beyond the scope of this paper.

Results

GAM provided generally good performance with median κ values above 0.63 on the evaluation data set (lower quartile = 0.54; upper quartile = 0.72). With these models, if climate changed as projected by the GCM used in this paper, an optimized reserve system for current conditions could face a loss of ~6–11% of modelled plant species in a 50-year period (Table 2). Projected loss of species' representation would be greater with the no-dispersal scenario and with

Table 2 Percentage species' representation in the present (1961–1990) and future (2021–2050) within six theoretical reserve networks and a seventh random set of reserves in Europe

No.	Method (315 areas)	Present	Future		$\Delta_{\text{dispersal}}$
			No dispersal	Universal dispersal	
1	Presence*	100	92.92 (0.21)	93.94 (0.17)	1.02
2	Presence clustered*	100	88.88 (1.08)	92.15 (0.55)	3.27
3	Presence threshold*	100	93.45 (0.14)	94.47 (0.08)	1.02
4	Goal gap (0.97)	100	92.99	93.82	0.83
5	Goal gap (0.85) clustered	100	92.55	92.68	0.13
6	Goal gap (0.86) threshold	100	92.58	93.67	1.09
	Δ_{method}	–	4.57	2.32	–
7	Random [†]	99.33 (99.75)	89.02 (90.44)	92.88 (93.58)	

Two species responses to climate change are considered: no dispersal and universal dispersal. Variability in the results is calculated through a simple delta statistic ($\Delta = \text{max representation} - \text{min representation}$).

*Mean (SD, after 10 simulations).

[†]Mean ($P < 0.05$, after 1000 simulations).

clustered-reserve solutions. Simultaneously, loss of species' representation within selected reserves was projected to be lower with the universal-dispersal scenario and with suitability threshold-based reserve-selection approaches.

Uncertainties, or variability of expected species' representation within reserves (e.g. Araújo, 2004), were ~6% being 1–3% associated to variability in the dispersal assumptions and 2–5% associated to variability in the reserve-selection methods analysed tested (Table 2). Clustered reserves obtained levels of species' representation in the year 2050 that were no different (for the no-dispersal scenario) or lower (for the universal-dispersal scenario) than expected by chance ($P < 0.05$). Probability-based methods identified reserve networks with loss of representation generally similar to that obtained in reserve networks selected with presence-based methods.

A closer inspection of the data reveals that ~5% of the 1200 plant species modelled in this study (i.e. 58) are expected to lose their entire European-climate envelope during the reported period. In other words they would potentially go extinct regardless of the reserve-selection strategy used, given that current environmental conditions known to be suitable for their persistence are projected to disappear in the studied area. A further 2% of the species (i.e. 19) would still have suitable environmental conditions for persistence in Europe but these would not overlap spatially with current conditions. For these species to persist they would need to disperse and establish into new suitable areas, which might be a challenge for many of them. In other words, current reserve networks would not be adequate for these species unless they were able to move across the matrix, there were new conservation areas selected as stepping stones for dispersal, or there were population-translocation strategies in place. Ninety-three per cent of the species modelled (i.e. 1123) were projected to have varying degrees of overlapping distributions. For these species, reserve networks could be identified so that both current-predicted and future-projected occurrences were represented within reserves (see also Hannah & Salm, 2003). With these data it would be possible to represent all 93% of these species in the two time periods with only 68 grid cells. Naturally, persistence of species with nonoverlapping distributions could not be guaranteed with such a network.

Species projected to lose their climatic envelope occur mainly in southern Europe (including the Alps) and Scandinavia (including the Baltic states) (Fig. 1c). Species with nonoverlapping distributions follow similar pattern of richness, although Hungary – perhaps because of its flat topography, e.g. Peterson (2003) – is

highlighted to have a disproportionately higher density of species with nonoverlapping distributions in the two periods (Fig. 1b). If richness scores among species facing lower challenges for persistence (those with overlapping distributions) are overlaid with richness scores of species facing greater challenges for persistence (those with nonoverlapping distributions and those projected to lose their environmental envelope), then broad regions depicting expected levels of species' vulnerability within reserves are identified (Fig. 1d). It

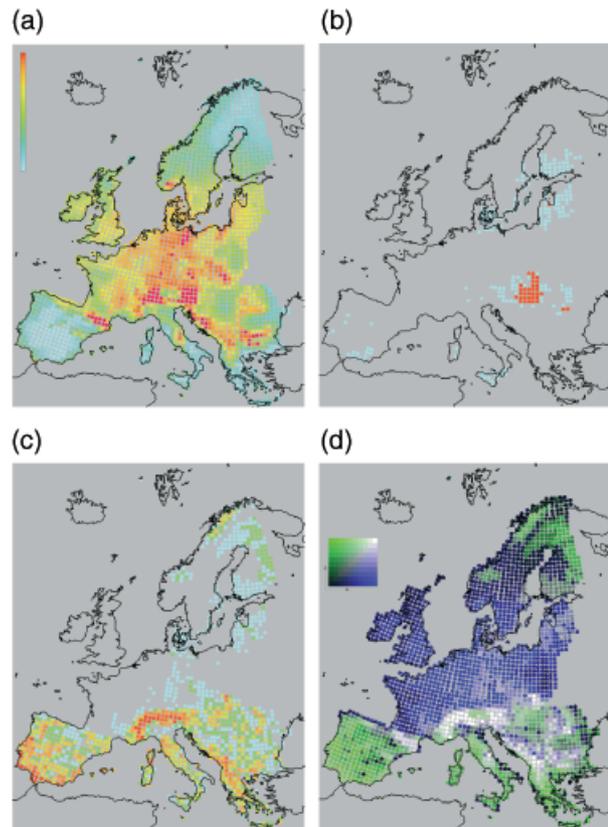


Fig. 1 European map of (a) richness among plant species modelled to have a degree of overlapping distributions in the two-time periods considered; (b) richness among plant species modelled to have nonoverlapping distributions in the two-time periods; (c) richness among plant species modelled to lose their entire climate envelope in the second period considered; (d) overlay between (a) and (b) + (c). Scores in (d) are divided into 10 colour-scale classes, where increasing intensities of blue represent increasing intensities of richness scores among species in (a), i.e. facing lower challenges for persistence and increasing intensities of green represent increasing of richness scores among species in (b) + (c), i.e. facing greater challenges for persistence. Black grid cells show low scores for richness in both (a) and in (b) + (c); white grid cells show high scores for both (a) and (b) + (c); and shades of grey show linearly covarying scores for both.

is shown (green on the map) that the European Mediterranean and parts of Scandinavia are the regions in Europe where plant-species conservation in reserves would be more challenged if the current climate-change scenario were realistic.

Discussion

We asked whether we should expect climate change to drive species out of reserves, if areas were not purposely selected to account for climate-change impacts on biodiversity. The answer is clearly yes. A loss of 6–11% of the bioclimatic range of 1200 modelled plant species within European theoretical reserve networks was estimated for a particular 50-year time period, subject to climate change. We also showed that climate change could lead to a species range loss within European reserves whatever reserve-selection strategy was adopted. This was the case for nearly 5% of the 1200 European-modelled plant species, which were projected to lose their entire climate envelope during the reported 50-year time period. Unless environmental tolerances of species were greater than measured (a possibility since we did not measure species' entire climate envelopes – for broad discussion of uncertainties associated with bioclimatic modelling see [Pearson & Dawson, 2003](#)), the long-term survival of these species could only be ensured through population translocation or *ex situ* conservation.

Among the remaining species, 93% were projected to maintain some degree of overlap in their distributions, while 2% were projected to have nonoverlapping distributions in the two time periods. The performance of existing reserve-selection methods to secure future distributions of species varied, suggesting that the choice of reserve-selection method is an important matter when designing reserve networks for climate change. Two lessons could be extracted from our analysis. The first is that selecting areas in currently suitable habitats for species, at the core of their environmental distributions, is more robust than selecting areas without consideration of habitat suitability (for extended discussion see [Araújo & Williams, 2001](#); [Araújo, 2002](#)). Nevertheless, this observation is likely to be contingent on the particular time period considered and the magnitude of environmental changes in the region. When environmental changes are weak, range dynamics might be determined predominantly by intrinsic population dynamics as described, for example, by [Lawton \(1993\)](#) and [Pimm \(1996\)](#). This is a core-periphery model in which populations located in highly suitable habitats (core) are predicted to be less sensitive to local demographic stochasticity than populations located in poor (margin-

al) habitats. However, when environmental changes are strong, species distributional dynamics might be driven heavily by these changes. New suitable areas might emerge in what were previously unsuitable or marginal habitats and previously suitable areas might be converted into unsuitable or marginal ones. In such circumstances, selection procedures that base reserve-prioritization on current assessments of habitat suitability are likely to target areas where species have low probabilities of persistence in the longer term. The period of time that would be necessary for this prediction to occur is still unknown. For this particular region and for the 50-year time period considered, currently suitable areas were correlated with future suitability to a certain degree. Similar results were obtained for another 20-year time period with breeding birds in Great Britain ([Araújo *et al.*, 2002a](#)). It is possible that changes occurring in the period of 2071–2100 – projected to be greater than for 2021–2050 ([Nakicenovic & Swart, 2000](#)) – will change current areas of suitability for species by an order of magnitude and that this will invalidate persistence expectations of current threshold-based reserve-selection strategies. Further analyses are needed to investigate this possibility.

The second lesson is that adding rules for reserve clustering may not necessarily improve species persistence in a climate-change context when compared, for example, with reserves selected with the sole goal of maximizing species representation. The reasons may be twofold. First, by adding rules to obtain clustered reserves we are trading off shape of reserves with species representation. In other words, representation-driven algorithms seek to maximize the number of occurrences of species within reserve networks, whereas reserve-clustering algorithms compromise potential increases in species representation by decreases in reserve boundary length. The result is that reserve networks are less scattered, but tend to show a greater degree of compositional redundancy. Given that clustering of reserves is proposed for the particular case where local extinctions are associated with genetic isolation, metapopulations, or edge effects near reserve boundaries, it is unsurprising to find that this strategy might perform poorly when modelled drivers of species loss are not governed by any of these factors but by directional environmental pressures. Second, by constraining algorithms to cluster reserves around particular nodes of endemism and richness (e.g. around mountain ranges) we are trading off the size of individual reserves with spanning of geographical and environmental conditions represented in reserve networks. If climate-change-induced species' extinctions were distributed randomly in space, then reserve networks spanning a broader geographical extent

would have greater probabilities of securing species than clustered reserves due to chance events alone. On the other hand, if species' extinctions were spatially structured (as seems to be the case), then clustering reserves on particular range-retention areas (areas of temporal overlap in species' distributions) would be advisable. But this provides a radical shift in the way clustering is performed, as it changes the focus from a trade-off between efficiency and reserve boundary to a new trade-off including assessments of local species' vulnerability to climate change.

Existing reserve-selection methods could easily be adapted to ensure species' persistence in such range-retention areas (see also Hannah & Salm, 2003). With our data, only 68 of such areas would be needed to represent all species with overlapping distributions in the two time periods. These range-retention areas could be treated as future refugia if species environmental niches were projected to overlap in space for long enough a period of time (Pitelka, 1997). However, for species with distributions projected to not overlap in time, current methods are clearly inadequate. In such cases, persistence will only be guaranteed if species are able to move between suitable areas. New-generation reserve-selection methods accounting for dispersal needs of species will be required if persistence of species with nonoverlapping distributions in time is to be sought (Williams *et al.*, in review).

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References

Andelman S, Ball I, Davis FW *et al.* (1999) *Sites V.1.0: An Analytical Toolbox for Designing Ecoregional Conservation Portfolios*. University of California, Santa Barbara.

Araújo MB (2002) Biodiversity hotspots and zones of ecological transition. *Conservation Biology*, **16**, 1662–1663.

Araújo MB (2004) Matching species with reserves: uncertainties from using data at different resolutions. *Biological Conservation*, **118**, 553–558.

Araújo MB, Williams P (2000) Selecting areas for species persistence using occurrence data. *Biological Conservation*, **96**, 331–345.

Araújo MB, Williams PH (2001) The bias of complementarity hotspots toward marginal populations. *Conservation Biology*, **15**, 1710–1720.

Araújo MB, Williams PH, Fuller RJ (2002a) Dynamics of extinction and the selection of nature reserves. *Proceedings of the Royal Society London, Biological Series*, **269**, 1971–1980.

Araújo MB, Williams PH, Turner A (2002b) A sequential approach to minimise threats within selected conservation areas. *Biodiversity and Conservation*, **11**, 1011–1024.

Ball I (2000) *Mathematical applications for conservation ecology: the dynamics of three hollows and the design of nature reserves*. PhD thesis. The University of Adelaide, Adelaide, Australia.

Bartlein PJ, Prentice IC, Webb T (1986) Climatic response surfaces from pollen data for some eastern North American taxa. *Journal of Biogeography*, **13**, 35–57.

Briers RA (2002) Incorporating connectivity into reserve selection procedures. *Biological Conservation*, **103**, 77–83.

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

Cabeza M, Araújo MB, Wilson RJ *et al.* (2004a) Combining probabilities of occurrence with spatial reserve design. *Journal of Applied Ecology*, **41**, 252–262.

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

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

Cabeza M, Moilanen A, Possingham HP (2004b) Metapopulation dynamics and reserve network design. In: *Metapopulation Ecology, Genetics, and Evolution* (eds Hanski I, Gaggiotti O), Academic Press, New York.

Church RL, Stoms DM, Davis FW (1996) Reserve selection as a maximal covering location problem. *Biological Conservation*, **76**, 105–112.

Cowling RM, Pressey RL, Lombard AT *et al.* (1999) From representation to persistence: requirements for a sustainable system of conservation areas in the species-rich Mediterranean-climate desert of southern Africa. *Diversity and Distributions*, **5**, 51–71.

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

Hannah L, Midgley GF, Millar D (2002) Climate change-integrated conservation strategies. *Global Ecology and Biogeography*, **11**, 485–495.

Hannah L, Salm R (2003) Protected areas and climate change. In: *Climate Change and Biodiversity: Synergistic Impacts* (eds Hannah L, Lovejoy T), pp. 91–100. Conservation International, Washington, DC.

Higgins SI, Richardson DM (1999) Predicting plant migration rates in a changing World: the role of long-distance dispersal. *The American Naturalist*, **153**, 464–475.

Hopkinson P, Travis JMJ, Evans J *et al.* (2001) Flexibility and the use of indicator taxa in the selection of sites for nature reserves. *Biodiversity and Conservation*, **10**, 271–285.

- Hughes L (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution*, **15**, 56–61.
- Hutchinson GE (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 145–159.
- Jalas J, Suominen J (1972–1996) *Atlas Florae Europaeae*. The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki.
- Lahti T, Lampinen R (1999) From dot maps to bitmaps – *Atlas Florae Europaeae* goes digital. *Acta Botanica Fennica*, **162**, 5–9.
- Lawton JH (1993) Range, population abundance and conservation. *Trends in Ecology and Evolution*, **6**, 409–413.
- Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237–240.
- MacArthur RH, Wilson EO (1963) An equilibrium theory for insular zoogeography. *Evolution*, **17**, 373–387.
- Malthus TR (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*. J. Jonhson, in St. Paul's Church-yard, London.
- Margules CR, Nicholls AO, Pressey RL (1988) Selecting networks of reserves to maximise biological diversity. *Biological Conservation*, **43**, 63–76.
- Margules CR, Nicholls AO, Usher MB (1994) Apparent species turnover, probability of extinction and the selection of nature reserves: a case study of Ingleborough limestone pavements. *Conservation Biology*, **8**, 398–409.
- Margules CR, Pressey RL (2000) Systematic conservation planning. *Nature*, **405**, 243–253.
- Mitchell TD, Carter TR, Jones PD *et al.* (2004) A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1901–2000) and 16 scenarios (2001–2100). *Journal of Climate Research* (in press).
- Moilanen A, Cabeza M (2002) Single-species dynamic site selection. *Ecological Applications*, **12**, 913–926.
- Monserud RA, Leemans R (1992) Comparing global vegetation maps with the Kappa statistic. *Ecological Modelling*, **62**, 275–293.
- Nakicenovic N, Swart R (2000) *Emissions Scenarios: A Special Report of Working Group III of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.
- Nicholls AO, Margules CR (1993) An upgraded reserve selection algorithm. *Biological Conservation*, **64**, 165–169.
- Onal H, Briers RA (2002) Incorporating spatial criteria in optimum reserve network selection. *Proceedings of the Royal Society London, Biological Series*, **269**, 2437–2411.
- Parmesan C, Ryrholm N, Stefanescu C *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 578–583.
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Pearson RG, Dawson TE (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- Peters RL, Darling JD (1985) The green-house effect and nature reserves. *BioScience*, **35**, 707.
- Peterson AT (2003) Projected climate change effects on Rocky Mountain and Great Plain birds: generalities of biodiversity consequences. *Global Change Biology*, **9**, 647–655.
- Peterson AT, Ortega-Huerta MA, Bartley J *et al.* (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature*, **416**, 626–629.
- Pimm SL (1996) Community stability and structure. In: *Conservation Biology: The Science of Scarcity and Diversity* (ed. Soulé M), pp. 309–329. Sinauer, Massachusetts.
- Pitelka F (1997) Plant migration and climate change. *American Scientist*, **85**, 464–473.
- Possingham HP, Ball I, Andelman S (2000) Mathematical methods for identifying representative reserve networks. In: *Quantitative Methods for Conservation Biology* (eds Ferson S, Burgman M), pp. 291–305. Springer-Verlag, New York.
- Prentice IC, Cramer W, Harrison SP *et al.* (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography*, **19**, 117–134.
- Pulliam HR (1988) Sources, sinks, and population regulation. *The American Naturalist*, **132**, 652–661.
- Rodrigues AS, Gregory RD, Gaston KJ (2000) Robustness of reserve selection procedures under temporal species turnover. *Proceedings of the Royal Society of London, Biological Series*, **267**, 49–55.
- Root TL, Price JT, Hall KR *et al.* (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.
- Scott D, Malcolm JR, Lemieux C (2002) Climate change and modelled biome representation in Canada's national park system: implications for system planning and park mandates. *Global Ecology and Biogeography*, **11**, 475–484.
- Segurado P, Araújo MB (2004) An evaluation of methods for modelling species distributions. *Journal of Biogeography* (in press).
- Shaffer CL (2001) Inter-reserve distance. *Biological Conservation*, **100**, 215–227.
- Sykes MT, Prentice IC (1996) Climate change, tree species distributions and forest dynamics: a case study in the mixed conifer/northern hardwoods zone of northern Europe. *Climatic Change*, **34**, 161–177.
- Thomas CD, Lennon JJ (1999) Birds extend their ranges northwards. *Nature*, **399**, 213.
- Thuiller W (2003) BIOMOD: optimising predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, **9**, 1353–1362.
- Thuiller W, Brotons L, Araújo MB *et al.* (2004) Effects of restricting environmental range of data to project current and future species distributions. *Ecography*, **27**, 165–172.
- Virolainen KM, Virola T, Suhonen J *et al.* (1999) Selecting networks of nature reserves: methods do affect long-term outcome. *Proceedings of the Royal Society of London, Biological Series*, **266**, 1141–1146.
- Warren MS, Hill JK, Thomas JA *et al.* (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.
- Williams PH (1999) *WORLDMAP 4 Windows: Software and Help Document 4.2*, London (Distributed privately).
- Williams PH, Araújo MB (2000) Using probability of persistence to identify important areas for biodiversity conservation. *Proceedings of the Royal Society London, Biological Series*, **267**, 1959–1966.

- Williams PH, Araújo MB (2002) Apples, oranges, and probabilities: integrating multiple factors into biodiversity conservation with consistency. *Environmental Modeling and Assessment*, **7**, 139–151.
- Williams PH, Hannah L, Andelman S *et al.* (2004) Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology* (in press).
- Williams PH, Humphries C, Araújo MB *et al.* (2000) Endemism and important areas for representing European biodiversity: a preliminary exploration of atlas data for plants and terrestrial vertebrates. *Belgian Journal of Entomology*, **2**, 21–46.
- Williams PH, Moore JL, Toham AK *et al.* (2003) Integrating biodiversity priorities with conflicting socio-economic values in the Guinean–Congolian forest region. *Biodiversity and Conservation*, **12**, 1297–1320.
- Woodroffe R, Ginsberg J (2000) Ranging behaviour and vulnerability to extinction in carnivores. In: *Behaviour and Conservation* (eds Gosling LM, Sutherland WJ), pp. 125–140. Cambridge University Press, Cambridge.
- Woodward FI (1987) *Climate and Plant Distribution*. Cambridge University Press, Cambridge.