A sequential approach to minimise threats within selected conservation areas

MIGUEL B. ARAÚJO[1,2,4,*], PAUL H. WILLIAMS[1] and ANDY TURNER[3]

[1]*Biogeography and Conservation Laboratory, The Natural History Museum, London SW5 5BD, UK;*
[2]*Centre of Applied Ecology, University of Évora, Largo dos Colegiais 7000 Évora, Portugal;* [3]*Centre for Computational Geography, School of Geography, University of Leeds, Leeds LS2 9JT, UK;* [4]*Current address: Centre D'Écologie fonctionelle, CNRS, 1919 Route de Menne, 34293 Montpellier Cedex 5, France;* [*]*Author for correspondence (e-mail: mba@uevora.pt)*

Abstract. Core–periphery models allow predictions of persistence to be made with relatively little data. The rationale is that populations in the core of their geographical or ecological ranges occupy suitable habitats and exhibit higher and less variable densities. Populations along the peripheries tend to be more fragmented and therefore less likely to receive immigrants from other populations. A population's probability of persistence is expected to correlate positively with habitat suitability and immigration rate and to correlate negatively with demographic variability. These predictions may be invalidated by the effect of threats, which may cause some peripheral populations to persist rather than populations in the core. We expect that predictions of persistence from core–periphery models will be improved by incorporating information on threats, and illustrate one way in which threat could be integrated within quantitative area-selection methods. We illustrate this for Europe by showing that important areas for biodiversity, selected with presence data, have consistently more people than expected by chance, but that incorporating human density as a constraint to area selection can reduce substantially this level of pressure. We also show that areas selected using simple core–periphery models have fewer people than areas selected with presence data only. These results support the idea that there are opportunities to identify important areas for the persistence of species that are located in areas with low human density.

Introduction

Conservation area networks ought to be located where species are more likely to persist. The problem is that knowledge of the local population dynamics for many species is poor, with the result that conservation-planning decisions are usually forced to rely on coarse surrogate measures that are expected to correlate with persistence.

As an example of a surrogate for information on population dynamics, it might be better to select conservation areas in high quality habitats from within the geographical core of species ranges. This is because these areas are expected to support higher abundances (e.g. Whittaker 1967; Hengeveld and Haeck 1981; Rapoport 1982; Brown 1984; Caughley et al. 1988; Lawton 1995) and be more resilient to demographic stochasticity (Curnutt et al. 1996). Lower habitat quality and greater

isolation at the edge of the ranges mean that populations may be extremely difficult to maintain in the near future. One approach is to attempt to model habitat quality and isolation from presence–absence data. For example, patterns of aggregation among species' occurrence records can be used to predict abundance at finer scales (e.g. Kunin 1998), which in turn relates to the amount of resources available, and to the ability of species to disperse from one area to another (Gonzalez et al. 1998). Occurrence records can also be used to fit more explicit niche-based suitability models (Araújo and Williams 2000). Populations in the core of this environmental space are expected to be more abundant and resilient to environmental stochasticity (e.g. Hutchinson 1957; Whittaker 1967; Hengeveld 1992). In many cases, geographically marginal populations are also ecologically marginal (Lesica and Allendorf 1995).

However, geographical patterns of threat (defined as extrinsic human and stochastic natural events occurring in a given area and time) may invalidate these predictions. Indeed, empirical observations of geographic range collapse for a broad range of taxonomic groups and geographical regions show that isolated populations often persisted when populations at the core of the range were extirpated (Lomolino and Channell 1995; Channell and Lomolino 2000a, b). This is because threats are often spatially autocorrelated (e.g. McCarthy and Lindenmayer 2000), with the result that extinctions may progress contagiously, like a disease, across geographical space. Regardless of where contagion begins, the last place affected may be the region most isolated from the initial extinction and this is likely to be along an edge of the range (Channell and Lomolino 2000b). In addition, the impact of contagion among threats may be higher in dense and interconnected populations at the core than in isolated populations within the range margins (Burgman et al. 1993; Lomolino and Channell 1995).

Araújo and Williams (2000) proposed a conceptual framework to deal with problems of persistence in area selection, which was shown to improve persistence over methods that use species' occurrence data only (Araújo et al., under review). The framework starts by fitting probabilistic models to explain the occurrence of species in terms of factors that are expected to affect the favourability of sites for species (e.g. habitat suitability and/or potential for dispersal). Estimates of site quality may then be combined with available information on extrinsic threats and species' vulnerability to those threats to provide an assessment of extinction risk. Finally, optimising area-selection techniques are applied to identify representative conservation area networks that maximise the likelihood of persistence among species. The framework is expected to overcome some of the shortcomings of simple core–periphery models for species persistence, because it explicitly incorporates the effect of threats and individual species' responses to them in the predictions. The critical issue, however, is that the relationship between site quality, expected threats and vulnerability is generally unknown or unpredictable, with the result that estimates of persistence may have to rely on site quality alone (Araújo and Williams 2000; Araújo et al., under review). This is an important shortcoming of the methods, given that threat and vulnerability are often perceived as major driving forces for setting priorities in real-world conservation planning. For example, in

Table 1. Description of the European data set of plants and terrestrial vertebrates.

Taxa	No. of species	No. of records	Median range sizes	Source
Plants	2362	462 925	28	Jalas and Suominen 1972, 1973, 1976, 1979, 1980, 1983, 1986, 1989, 1991, 1994, 1996
Mammals	187	81 309	187	Mitchell-Jones et al. 1999
Breeding birds	445	291 390	389	Hagemeijer and Blair 1997
Reptiles	149	34 137	82	Gasc et al. 1997

southern Sweden, consideration of threats to areas contributed to the establishment of at least 40% of the protected areas (Emneborg and Götmark 2000).

Here, we discuss one simple approach to integrating information on threats in order to improve upon estimates of persistence from the simplest geographical (or environmental) core–periphery models. In this particular case we use human population density as a surrogate for threat and assume that all species are equally affected by threats. The approach uses sequential (non-compensatory) techniques to select areas at the core of species ranges while minimising the level of threat, i.e. as indicated by the number of people, within selected areas. We illustrate this using a large data set for the distribution of plant, mammal, bird, reptile and amphibian species in Europe (Table 1). The sequential approach outlined here is not a substitute for more elaborate predictive models of persistence, but it does provide a first approximation to the problem of persistence when area-selection decisions have to be made in the absence of more complete information for large numbers of species. In such cases, even crude estimates of persistence using available data could guide area-selection decisions in a way that is expected to be more effective than treating all areas and all species as equal, or simply discriminating areas by their position within the species' geographical (or environmental) space.

In addition, we ask: (1) Do important areas for biodiversity in Europe have more people within them than expected by chance? (2) Do methods that select areas preferentially from within the core of a species' range have significantly fewer people than areas selected with presence data alone?

Combining factors to estimate persistence

Populations persist if the net increase of individuals in an area (i.e. birth and immigration rates) exceeds the net loss (i.e. death and emigration rates). In practice it is difficult to obtain detailed population parameters when large numbers of species and areas are involved. A possible strategy is to establish environmental and socio-economic correlations of these parameters and combine them in some logical way. For example, habitat suitability is expected to correlate positively with birth rates, whilst the added risk resulting from combining extrinsic threats with species vulnerabilities is expected to correlate with death rates. Similarly, proximity of populations is expected to correlate with the ability of species to disperse from one area to another and therefore to establish stable metapopulation dynamics. Multi-

criteria decision models offer two alternative strategies to combine criteria and produce a ranking among alternatives: *composite* (compensatory) and *sequential* (non-compensatory) approaches (e.g. Hwang and Yoon 1981; Smith and Therberge 1987).

Composite approaches

Composite approaches often involve some form of addition or multiplication of criteria (e.g. Tubbs and Blackwood 1971; Goldsmith 1975; Ward and Evans 1976; Adamus and Clough 1980; Williams 1980; Dony and Denholm 1985). However, if criteria are not comparable, then it might be difficult to justify combination of values into a single number (e.g. Järvinen 1985; Götmark et al. 1986; Given and Norton 1993; Williams 1998). Even when criteria are related (e.g. threat to areas and vulnerability to threats) they may not be inter-convertible, since currencies and measurement scales used are different. If score ranges were standardised to comparable units of measurement (e.g. to zero means and unit variances), this would still imply a transformation with no particular biological justification or meaning (Smith and Therberge 1987).

An alternative approach proposes that the conversion of factors related to persistence could be derived empirically using a probabilistic framework (Williams and Araújo 2000). This would offset some of the inherent arbitrariness of the most traditional combinatorial approaches and provide a consistent framework to combine multiple species information in a common currency of conservation success, i.e. probabilities of persistence. However, useful estimates of species' probabilities of persistence are difficult to obtain for a single species in a single area (e.g. Harcourt 1995), let alone for a large number of species and areas (e.g. Ludwig 1999). A possibility would be to use generalised linear or additive models to seek combinations of factors that govern current probabilities of occurrence of species and use these as estimates of persistence in the near future (Araújo 2000). The assumption is that many of the factors affecting current occurrences (e.g. habitat suitability, dispersal and past threats) would not be independent from those affecting future occurrences. If threats were included in the models, along with other variables affecting occurrences, then models would be expected to reflect the responses of species to threats as well as to the other components. However, this would only be true if current distributions were in equilibrium with past threats (i.e. absent within areas with high threats and present within areas with low threats). Otherwise, any relationship between threats and species' occurrences might be obscured.

Sequential approaches

Sequential approaches are designed to combine criteria of different currencies and measurement scales (e.g. Goldsmith 1987; Bedward et al. 1992; Williams 1998). Alternatives are assessed criterion by criterion, in a sequential way, so that no multiplication or addition is needed. This has advantages over composite approaches in that no explicit assumptions have to be made about the quantitative

function linking the factors, although the sequence with which factors are combined imposes an order of precedence that may not always be justifiable. Nevertheless, sequential approaches preserve accountability since the reasons why species or areas have been included or excluded at each step of the analysis can be monitored easily. This might be a considerable advantage since uncertainty (or ignorance) is explicit rather than being buried in some elaborate, but essentially arbitrary composite index. Sequential approaches that use filters have an additional advantage of favouring top ranking values for each criterion. As a result only areas with high scores for values and low scores for penalties or constraints are selected. If instead composite approaches are used, then the overall assessment may favour areas with high combined values for criteria, which may include medium or even low values for individual criteria. This may result in area networks that are not particularly good for any individual criterion, but which score highly overall. Here, we use a sequential (non-compensatory) approach that maximises species representation in conservation area networks, while maximising habitat suitability and minimising threat.

Methods

Measurement of threat

Human-induced threats constitute the primary causes of endangerment and extinction of many species (e.g. May et al. 1995; Pimm et al. 1995). They include land development (e.g. habitat destruction, degradation and fragmentation), overexploitation (e.g. fisheries, hunting and international trade) and introduction of exotic species (Lande 1998). Therefore, variables measuring the degree of human interference to areas can be used as indicators of threat to biodiversity (e.g. Hannah et al. 1994; Forester and Machlis 1996; Reyers et al. 1998). Examples include human population density (e.g. Kerr and Currie 1995; Maurer 1996; Thompson and Jones 1999; Cincotta et al. 2000; Balmford et al. 2001), and other economic or demographic factors that imply a rate of consumption of biological resources such as road building, recreation, agriculture and urbanisation (e.g. Nantel et al. 1998; Cowling et al. 1999; Wessels et al. 2000).

Here, we use human population density surfaces for Europe as a surrogate for threat to species. This is thought to be one of the factors most closely related to extinction risk, especially for birds (Kerr and Currie 1995). Human population density surfaces were created in two stages; the first involved generating high-resolution estimates, and the second involved aggregating these high-resolution estimates. Population density estimates at one-decimal-minute resolution (approximately 1 km^2) were generated by interpolating available population data (for NUTS3 regions) using auxiliary data and neural networks (Openshaw and Turner 2001). These high-resolution estimates were then transformed to provide human population density estimates for UTM (Universal Transverse Mercator) 50 by 50 km grid cells. This could have been done in various ways. The approach used was an

iterative procedure that aggregated gradually to introduce less spatial bias in the aggregate estimates compared with the conventional one-step aggregation. This involved a repeated cycle of aggregation, re-sampling, combination and re-aggregation. The aggregation step involved generating four grids with cells of double the width and height. These were re-sampled and averaged at the starting resolution, then one of the aggregations was chosen to re-aggregate. This cycle was repeated until estimates were available for the chosen spatial framework. An alternative would have been to aggregate as normal, then generate a cross-scale density surface as described by Turner (2000).

Sequential approach to persistence

Species are expected to have higher probabilities of persistence (1) if they are represented from the core of their geographical or ecological ranges, and (2) if they are distributed in areas with reduced threats. As a first approximation, species are assumed to be equally vulnerable to threats (for a similar treatment of threat and vulnerability see Faith and Walker 1996), so that areas with high scores for threat are excluded from selection regardless of each individual species' responses to them.

Geographical patterns of range core–periphery were estimated using a measure of contagion (i.e. the degree of aggregation among species' individual records). When dealing with occurrence records within grid cells, contagion can be measured as:

$$Contagion = \left(\frac{\sum_{b=1}^{k_a} w_{ab} y_b}{\sum_{b=1}^{k_a} w_{ab}} \right) \times 100 \qquad (1)$$

where contagion is a weighted average of the number of occupied grid cells among a set of k_a neighbours of a central grid cell y_a. The weight given to the grid cell y_b is $w_{ab} = 1/d_{ab}$, where d_{ab} is the distance between grid cells y_a and y_b. We used two orders of neighbours, assigning a weight of $d = 1$ to the first-order and a weight of $d = 2$ to the second-order neighbours. Neighbours in the first order were the eight adjacent cells touching the central cell along the edges and at the corners within a rectangular grid. The second-order neighbours were the next group of cells concentric to first order with 16 grid cells.

Contagion index values range between 0 and 100% of the maximum aggregation possible. Maximum aggregation is expected to occur within the 'core' and minimum values are expected to occur within the 'margins' of a species' range. Because values are assigned to any grid cell with occupied neighbours up to the second-order neighbourhood, areas with contagion values but no records were excluded from the area-selection exercise. Contagion models correlate with and are therefore expected to be good surrogates for computationally more expensive environmental core–periphery models (Araújo and Williams 2000, 2001; Araújo et al., under review).

An example of the proposed sequential approach to area selection is provided

using distribution atlas data for European terrestrial vertebrate and plant species (Table 1). A full description of the data is provided by Williams et al. (2000) and Araújo et al. (2001).

Both common forms of quantitative area-selection problems are considered. The first is the 'minimum-set problem', such as 'what is the minimum cost required to represent all species a given number of times?'. The second is the 'maximum-coverage problem', such as 'what degree of species representation can be achieved for a given budget?'. Minimum-set approaches are useful to assess selection strategies in terms of cost-efficiency. Maximum-coverage approaches are useful to assess strategies for their performance to achieving conservation targets.

The sequential approach to threat adopted here (hereafter referred to as core-threat method) uses a similar stepwise approach as proposed by Araújo and Williams (2000), but with two additional steps (steps 2 and 3) to reduce threats within the selected areas. Step 1: exclude all individual species records with suitability scores (here contagion) lower than a specified threshold. To guarantee that all species i are selected from their relative local 'core' areas a, suitability scores (S) are re-scaled to ensure that each species occupies the full range of values 0–1. The threshold is then applied (here, $S_{i,a} > 0.95$) so that the selection algorithm 'sees' only the best areas (i.e. with highest contagion) for each species, regardless of their absolute values. Step 2: for each species, records with threat scores higher than a specified threshold (here, $S_a > 0.95$) are set to zero. This ensures that each species is selected only from areas with relatively lower threats within the most suitable parts of their ranges. Step 3: a minimum-set algorithm is applied to represent all species at least once. A slight modification over the traditional minimum-set approach is used so as to minimise the ratio threat/area, rather than simply area. This ensures that species are selected from areas with low threats relative to their biodiversity benefits.

Area-set solutions obtained with this approach are compared with solutions to three other problems for the same number of areas. The first is a maximum-coverage solution selected to maximise species representation from areas with top contagion scores for each individual species (i.e. step 1 followed by step 3 but without the threat minimisation procedure, hereafter referred to as core method). The second is a maximum-coverage solution that maximises species representation using presence data only [adapted from Margules et al. (1988), hereafter referred to as presence method]. The third is a method that simulates selecting a given number of areas with records at random. The selection is repeated 1000 times to calculate the 5% upper tail of the random distribution of threat values. This is used to test differences from observed values of threat within selected areas with those expected by chance ($P < 0.05$). All area-selection procedures were implemented using the package WORLDMAP (Williams 1999).

Results

Important areas for biodiversity in Europe are predominantly located in the south (Figure 1), coinciding closely with the distribution of Meyers et al.'s (2000)

Mediterranean biodiversity hotspots. Nevertheless, a number of conservation areas further north would still be needed if a full representation of species were sought.

If areas were selected to represent all selected species of European plants and terrestrial vertebrates from the most suitable and least threatened areas for each species, then a total of 492 areas would be needed across the study region (i.e. ca.

Figure 1. Important areas for biodiversity conservation in Europe as selected with four alternative quantitative approaches: (a) core-threat method; (b) core method; (c) presence maximum-coverage set; (d) presence near-minimum set.

20% of the total). In contrast, a near-minimum set using presence data only would require half of this number of areas (Table 2). The core-threat method is more expensive overall, because more areas are selected and more people are included overall. Nonetheless, the core-threat method affects fewer people per unit area than the near-minimum set (average 70528 against 107684 people per unit area) so that the pressure or conflict is spread more thinly, and tends to be lower in any one area. Because human density and other human-induced threats are expected to correlate positively with cost (e.g. cost of land acquisition, restoration and management, and opportunity costs), it is likely that conservation areas selected with this additional rule be also cheaper in a per area unit basis.

A comparison of the number of people within areas selected with the core-threat, the core, the presence, and the random selection methods (for 492 areas), shows that the number of people within areas is: core-threat method < core method < random selection < presence method (Table 2). It is not surprising that areas selected with the core-threat method have fewer people, since neither the core, the presence, nor the random methods seek to minimise people within areas. Perhaps of greater interest, the core-constrained solution has fewer people than the simple maximum-coverage solution using presence data only. This might imply that those areas that are currently more suitable for species (i.e. that have more aggregated populations) are also the areas that had proportionally lower threats in the past. To investigate this idea further and to check for consistency in these results, we selected 1000 fully flexible alternative sets for both methods and compared the mean number of people represented by the two methods. Flexible solutions for the presence method had a total average of 56201 million people (min. 54400; max. 58061) within areas, while the core method had a total average of 43605 million (min. 41116; max. 46471). This is consistent with the magnitude of differences in Table 2. A non-parametric test of difference between means also reveals that human population differs significantly between the core and presence methods (Wilcoxon test, two-tailed $P < 0.0001$).

Simulations of selecting areas at random show that both the core-threat and core methods have fewer people within them than expected by chance ($P < 0.05$). In contrast, the presence method includes more people than expected by chance ($P < 0.05$). These results suggest that important areas for biodiversity might coincide with areas that are also more favourable to humans, but that constraining selection to the most suitable areas for each species can reduce conflicts with people.

Table 2. Area-selection methods, number of areas selected, percentage of species represented and the total number of people (millions) within area sets.

Method	No. of areas selected	Representation (%)	No. of people
Core-threat near-minimum set	492	100	34700
Core maximum-coverage	492	100	45114
Presence, maximum-coverage	492	100	55914
Presence, near-minimum set	247	100	26598
Random selection[a]	492	79	50335

[a]$P < 0.05$.

Discussion

Simple sequential (non-compensatory) area selection approaches can offset some of the complications associated with modelling persistence from threats and vulnerabilities, if an assumption is made that all species respond in a similar way to threats. By ensuring that conservation areas are selected from the core of each species' geographical (or environmental) ranges and by simultaneously avoiding records with relatively high threats within each individual species' range, this method should select networks of areas that are more robust to extinctions, whether due to local natural stochasticity or to the included threats. Our approach is also expected to improve over methods that seek only to minimise threats (or conflicts) within selected areas (e.g. Nantel et al. 1998; Wessels et al. 2000), because there is some account of the intrinsic factors affecting species' persistence (Araújo and Williams 2000).

Nevertheless, the assumption that all species respond similarly to threats is a simplistic one. Some species may be extremely sensitive to particular human-induced threats, while others may adapt to intermediate levels of threat, or may even benefit from high levels of threat to other species. If information on individual species' responses to threats were available, then thresholds (step 2 of the proposed method) could be set differently for each species according to their varying degrees of tolerance to threats. This would be a relatively simple add-on to the method, which would make it more realistic in complex conservation planning decisions. However, the effect of excluding areas with high threat levels (e.g. human population) is most likely to benefit the most vulnerable species (i.e. species with low degrees of tolerance to humans). These are the species of highest conservation concern, which depend heavily on the conservation of the few spots that remain relatively undisturbed in Europe. In contrast, no major deleterious effect is likely to be felt by the least vulnerable species (i.e. species with high degrees of tolerance to humans), since these are generally widespread and may already co-exist with high levels of present-day disturbance. Therefore, the sequential approach to area selection proposed here (i.e. the core-threat method) is likely to improve upon the persistence prognoses obtained from simple core–periphery models (i.e. the core method). The proposed core-threat method should also produce networks of areas for conservation that are cheaper on a per unit area basis, because human-induced threats are often correlated with cost (e.g. McNeely 1996). However, the greater the number of penalties or constraints (e.g. threats) imposed on area selection, the greater the number of areas that are likely to be needed (e.g. Nicholls and Margules 1993; Nantel et al. 1998; Pressey and Logan 1998; Araújo and Williams 2000; Wessels et al. 2000). This implies an increase in the total cost of the network, which has to be considered against the improvements in the expected persistence of species.

We suspect, however, that the extent of the improvement in terms of increased persistence may not always be as great as our estimated expectations would imply. Indeed, if current distributions are already affected by past threats, then it is likely that the most vulnerable species would avoid threats or at least have their current

core populations away from the most threatened sites. A comparison of the results from using the core and presence area-selection methods supports this view, because the core method includes consistently fewer people (i.e. threats) than the presence method. We believe this is because the dynamic nature of species' ranges allows them to shift distributions according to the various factors affecting the suitability of areas. Even if there were a consistent pattern of a broad coincidence between favourable areas for humans and for other species (Balmford and Long 1994; Fjeldså and Rahbek 1998; Balmford et al. 2001), it is likely that species with lower degrees of tolerance to humans will have their core populations away from where people are concentrated in greater numbers. This is consistent with the idea of high diversity at intermediate levels of disturbance (for a review see Rosenzweig 1995), although it is likely that past extinctions may play an important role explaining at least part of this pattern. Indeed, if human disturbances have already filtered out many of the species that would be vulnerable to current threats (e.g. Balmford 1996), then it is possible that areas of high diversity will be located in areas with intermediate levels of disturbance. This would be simply because the most sensitive species presently occupying the least disturbed areas might already have been lost from much of Europe.

Acknowledgements

References

Adamus P.R. and Clough C.G. 1980. Evaluating species for the protection of natural areas. Biological Conservation 13: 165–178.

Araújo M.B. 2000. The representation and persistence of species in conservation areas network, Ph.D. Thesis, University of London.

Araújo M.B. and Williams P.H. 2000. Selecting areas for species persistence using occurrence data. Biological Conservation 96: 331–345.

Araújo M.B. and Williams P.H. 2001. The bias of complementarity hotspots toward marginal populations. Conservation Biology 15: 1710–1720.

Araújo M.B., Densham P.J., Lampinen R., Hagemeijer W.J.M., Mitchell-Jones A.J., Gasc J.P. et al. 2001. Would environmental diversity be a good surrogate for species diversity? Ecography 24: 103–110.

Balmford A. 1996. Extinction filters and current resilience: the significance of past selection pressure for conservation biology. Trends of Ecology and Evolution 11: 193–196.

Balmford A. and Long A. 1994. Avian endemism and forest loss. Nature 372: 623–624.

Balmford A., Moore J., Brooks T., Burgess N., Hansen L., Williams P. et al. 2001. Conservation conflicts across Africa. Science 291: 2616–2619.

Bedward M., Pressey R.L. and Keith D.A. 1992. A new approach for selecting fully representative reserve networks: addressing efficiency, reserve design and land suitability with an iterative analysis. Biological Conservation 62: 115–125.

Brown J.H. 1984. On the relationship between abundance and distribution of species. American Naturalist 124: 255–279.

Burgman M.A., Ferson S. and Akçakaya H.R. 1993. Risk Assessment in Conservation Biology. Population and Community Biology Series 12. Chapman & Hall, London.

Caughley G., Grice D., Barker R. and Brown B. 1988. The edge of the range. Journal of Animal Ecology 57: 771–785.

Channell R. and Lomolino M. 2000a. Dynamic biogeography and conservation of endangered species. Nature 403: 84–86.

Channell R. and Lomolino M. 2000b. Trajectories of extinction: spatial dynamics of the contraction of geographical ranges. Journal of Biogeography 27: 169–179.

Cincotta R.P., Wisnewski J. and Engelman R. 2000. Human population in the biodiversity hotspots. Nature 404: 990–992.

Cowling R.M., Pressey R.L., Lombard A.T., Desmet P.G. and Ellis G. 1999. From representation to persistence: requirements for a sustainable system of conservation areas in the species-rich Mediterranean-climate desert of South Africa. Diversity and Distribution 5: 51–71.

Curnutt J.C., Pimm S.L. and Maurer B.A. 1996. Population variability of sparrows in space and time. Oikos 76: 131–144.

Dony J.G. and Denholm I. 1985. Some quantitative methods of assessing the conservation value of ecologically similar sites. Journal of Applied Ecology 22: 229–238.

Emneborg E. and Götmark F. 2000. The role of threat to areas and initiative from actors for establishment of nature reserves in southern Sweden 1926–1996. Biodiversity and Conservation 9: 727–738.

Faith D.F. and Walker P.A. 1996. Integrating conservation and development: incorporating vulnerability into biodiversity assessment of areas. Biodiversity and Conservation 5: 417–429.

Fjeldså J. and Rahbek C. 1998. Continent-wide diversification processes and conservation priorities. In: Mace G., Balmford A. and Ginsberg J.R. (eds), Conservation in a Changing World: Integrating Process into Priorities for Action. Cambridge University Press, London, pp. 139–160.

Forester D.J. and Machlis G. 1996. Modelling human factors that affect the loss of biodiversity. Conservation Biology 10: 1253–1263.

Gasc J.-P., Cabela A., Crnobrnja-Isailovic J., Dolmen D., Grossenbacher K., Haffner P. et al. (eds) 1997. Atlas of Amphibians and Reptiles in Europe. Societas Europaea Herpetologica and Muséum National d'Histoire Naturelle, Paris.

Given D.R. and Norton D.A. 1993. A multivariate approach to assessing threat and for priority setting in threatened species conservation. Biological Conservation 64: 57–66.

Goldsmith F.B. 1975. The evaluation of ecological resources in the countryside for conservation purposes. Biological Conservation 8: 89–96.

Goldsmith F.B. 1987. Selection procedures for forest nature reserves in Nova Scotia, Canada. Biological Conservation 41: 185–201.

Gonzalez A., Lawton J.H., Gilbert F.S. and Blackburn T.M. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. Nature 281: 2045–2047.

Götmark F., Ahlund M. and Eriksson M.O.G. 1986. Are indices reliable for assessing conservation value of natural areas – an avian case study. Biological Conservation 38: 55–73.

Hagemeijer W.J.M. and Blair M.J. (eds) 1997. The EBCC Atlas of European Breeding Birds, Their Distribution and Abundance. Poyser (published for European Bird Census Council), London.

Hannah L., Lohse D., Hutchinson C., Carr J.L. and Lankerani A. 1994. A preliminary inventory of human disturbance of world ecosystems. Ambio 23: 246–250.

Harcourt A.H. 1995. Population viability estimates: theory and practice for a wild gorilla population. Conservation Biology 9: 134–142.

Hengeveld R. 1992. Dynamic Biogeography. Cambridge Studies in Ecology. Cambridge University Press, Cambridge, UK.

Hengeveld R. and Haeck J. 1981. The distribution of abundance, II. Models and implications. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen C84: 257–284.

Hutchinson G.E. 1957. Concluding remarks. Cold Spring Harbour Symposia on Quantitative Biology 22: 415–427.

Hwang C.-L. and Yoon K. 1981. Multiple Attribute Decision Theory, Methods and Applications: A State of the Art Survey. Springer-Verlag, Berlin.

Jalas J. and Suominen J. (eds) 1972, 1973, 1976, 1979, 1980, 1983, 1986, 1989, 1991, 1994, 1996. Atlas Florae Europaeae. Vols. 1–11. The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki,

Järvinen O. 1985. Conservation indices and land use planning: dim prospects for a panacea. Ornis Fennica 62: 101–106.

Kerr J.T. and Currie D.J. 1995. Effects of human activity on global extinction risk. Conservation Biology 9: 1528–1538.

Kunin W.I. 1998. Extrapolating species abundance across spatial scales. Science 281: 1513–1515.

Lande R. 1998. Anthropogenic, ecological and genetic factors in extinction. In: Mace G., Balmford A. and Ginsberg J.R. (eds), Conservation in a Changing World: Integrating Process into Priorities for Action. Cambridge University Press, London, pp. 29–50.

Lawton J.H. 1995. Population dynamic principles. In: Lawton J.H. and May R.M. (eds), Extinction Rates. Oxford University Press, Oxford, pp. 147–163.

Lesica P. and Allendorf F.W. 1995. When are peripheral populations valuable for conservation? Conservation Biology 9: 753–760.

Lomolino M.V. and Channell R. 1995. Splendid isolation: patterns of range collapse in endangered mammals. Journal of Mammalogy 76: 335–347.

Ludwig D. 1999. Is it meaningful to estimate a probability of extinction? Ecology 80: 298–310.

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

Maurer B.A. 1996. Relating human population growth to the loss of biodiversity. Biodiversity Letters 3: 1–5.

May R.M., Lawton J.H. and Stork N.E. 1995. Assessing extinction rates. In: Lawton J.H. and May R.M. (eds), Extinction Rates. Oxford University Press, Oxford, pp. 1–24.

McCarthy M.A. and Lindenmayer D.B. 2000. Spatially correlated extinction in a metapopulation model of Leadbeater's Possum. Biodiversity and Conservation 9: 47–63.

Mitchell-Jones A.J., Amori G., Bogdanowicz W., Kryštufek B., Reijnders P.J.H, Spitzenberger F. et al. 1999. Atlas of European Mammals. Academic Press, New York.

McNeely J.A. 1996. Assessing methods for setting conservation priorities Paper presented at OECD International Conference on Incentive Measures for Biodiversity Conservation and Sustainable Use, Cairns, Australia, 25–28 March 1996.

Myers N., Mittermeier R.A., Mittermeier C.G., Fonseca G.A.B. and Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Nantel P., Bouchard A., Brouillet L. and Hay S. 1998. Selection of areas for protecting rare plants with integration of land use conflicts: a case-study for the west coast of Newfoundland, Canada. Biological Conservation 84: 223–234.

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

Openshaw S. and Turner A. 2001. Disaggregative spatial interpolation. Paper presented at GSRUK, Wales. Available on-line at http://www.geog.leeds.ac.uk/staff/a.tuner/papers/gisruk01/gisruk01. htm (unpublished).

Pimm S.L., Russel G.J., Gittleman J.L. and Brooks T.M. 1995. The future of biodiversity. Science 269: 347–350.

Pressey R.L. and Logan V.S. 1998. Size of selection units for future reserves and its influence on actual

vs targeted representation features: a case study in western New South Wales. Biological Conservation 50: 199–218.

Rapoport E.H. 1982. Aerography: Geographical Strategies of Species. Pergamon, Oxford.

Reyers B., Jaarsveld A.S.V., McGeoch M.A. and James A.N. 1998. National biodiversity risk assessment: a composite multivariate and index approach. Biodiversity and Conservation 7: 945–965.

Rosenzweig M.L. 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge, UK.

Smith P.G.R and Therberge J.B. 1987. Evaluating natural areas using multiple criteria: theory and practice. Environmental Management 11: 447–460.

Thompson K. and Jones A. 1999. Human population density and prediction of local plant extinction in Britain. Conservation Biology 13: 185–189.

Tubbs C.R. and Blackwood J.W. 1971. Ecological evaluation for planning purposes. Biological Conservation 3: 169–172.

Turner A. 2000. Density data generation for spatial data mining applications. Paper presented at GeoComputation, England. Available on-line at http://www.geog.leeds.ac.uk/staff/a.turner/ papers/geocomp00/gc017.htm (unpublished).

Ward S.D. and Evans D.F. 1976. Conservation assessment of British limestone pavements based on floristic criteria. Biological Conservation 9: 217–233.

Wessels K.J., Reyers B. and Van Jaarsveld A.S. 2000. Incorporating land cover information into regional biodiversity assessments in South Africa. Animal Conservation 3: 67–79.

Williams G. 1980. An index for ranking of wildfowl habitats as applied to eleven sites in West Surrey, England. Biological Conservation 18: 93–99.

Williams P.H. 1998. Key sites for conservation: area-selection methods for biodiversity. In: Mace G., Balmford A. and Ginsberg J.R. (eds), Conservation in a Changing World: Integrating Process into Priorities for Action. Cambridge University Press, London, UK, pp. 211–249.

Williams P.H. 1999. WORLDMAP 4.1 WINDOWS: software and user document 4. Privately distributed, London. http://www.nhm.ac.uk/science/projects/worldmap (unpublished).

Williams P.H. and Araújo M.B. 2000. Using probability fo persistence to identify important areas for biodiversity. Proceedings of the Royal Society B 267: 1–8.

Williams P.H., Humphries C.J., Araújo M.B., Lampinen R., Hagemeijer W., Gasc J.-P. et al. 2000. Endemism and important areas for conserving European biodiversity: a preliminary exploration of atlas data for plants and terrestrial vertebrates. Belgium Journal of Entomology 2: 21–46.

Whittaker R.H. 1967. Gradient analysis of vegetation. Biological Reviews 42: 207–269.