
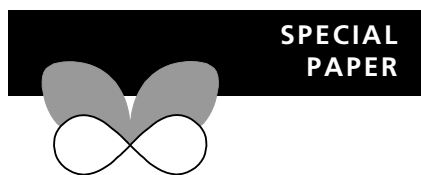
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Conservation Biogeography: assessment and prospect

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ABSTRACT

There is general agreement among scientists that biodiversity is under assault on a global basis and that species are being lost at a greatly enhanced rate. This article examines the role played by biogeographical science in the emergence of conservation guidance and makes the case for the recognition of Conservation Biogeography as a key subfield of conservation biology delimited as: *the application of biogeographical principles, theories, and analyses, being those concerned with the distributional dynamics of taxa individually and collectively, to problems concerning the conservation of biodiversity*. Conservation biogeography thus encompasses both a substantial body of theory and analysis, and some of the most prominent planning frameworks used in conservation. Considerable advances in conservation guidelines have been made over the last few decades by applying biogeographical methods and principles. Herein we provide a critical review focussed on the sensitivity to assumptions inherent in the applications we examine. In particular, we focus on four inter-related factors: (i) scale dependency (both spatial and temporal); (ii) inadequacies in taxonomic and distributional data (the so-called Linnean and Wallacean shortfalls); (iii) effects of model structure and parameterisation; and (iv) inadequacies of theory. These generic problems are illustrated by reference to studies ranging from the application of historical biogeography, through island biogeography, and complementarity analyses to bioclimatic envelope modelling. There is a great deal of uncertainty inherent in predictive analyses in conservation biogeography and this area in particular presents considerable challenges.

Protected area planning frameworks and their resulting map outputs are amongst the most powerful and influential applications within conservation biogeography, and at the global scale are characterised by the production, by a small number of prominent NGOs, of bespoke schemes, which serve both to mobilise funds and channel efforts in a highly targeted fashion. We provide a simple typology of protected area planning frameworks, with particular reference to the global scale, and provide a brief critique of some of their strengths and weaknesses. Finally, we discuss the importance, especially at regional scales, of developing more responsive analyses and models that integrate pattern (the compositionalist approach) and processes (the functionalist approach) such as range collapse and climate change, again noting the sensitivity of outcomes to starting assumptions. We make the case for the greater engagement of the biogeographical community in a programme of evaluation and refinement of all such schemes to test their robustness and their sensitivity to alternative conservation priorities and goals.

Keywords

Conservation biogeography, models, protected area frameworks, scale, sensitivity analysis, uncertainty.

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INTRODUCTION

Although biogeographical science has played its part alongside other subfields of biology in the emergence of current scientific

guidance for biodiversity conservation (e.g. Dasmann, 1972, 1973; Diamond, 1975), in our view it has done so as something of a poor relation — a Cinderella within Conservation Biology. In the present article, we argue that biogeography can now cast

aside its metaphorical rags as it emerges as an area of central importance to conservation planning. In part this has been driven by the advent of extensive computerised biogeographical data bases and powerful computer-based analytical tools, which have enabled rapid progress in many areas of the field, both pure and applied; and in part, it reflects theoretical and conceptual advances (e.g. Williams *et al.*, 2000a; Lomolino & Heaney, 2004).

Yet, we must also recognise that the underlying species distributional and other data often remain highly problematic, protocols for analysis are still in development, and we have only recently begun the task of systematically analysing the sensitivity of our analyses to the starting assumptions. Accordingly, we argue that there is a need for more biogeographers to get engaged with the problems of conservation science, and for the injection of more biogeography into training for conservation scientists (cf. Lourie & Vincent, 2004). As a step towards these goals, we first offer a definition of the field of *Conservation Biogeography*, placing it in the context of the closest surrounding disciplinary areas, and second, highlight what we believe to be key generic research needs within the field.

We are within a crucial phase in the development of conservation theory and strategy. There is general agreement that biodiversity is under assault on a global basis and that species are being lost at a greatly enhanced level (Lawton & May, 1995; Royal Society, 2003). In response, over the last decade, several prominent international non-governmental organisations (NGOs) have engaged in developing regional, continental, and particularly global schemes (e.g. Dinerstein *et al.*, 1995; Long *et al.*, 1996; Olson & Dinerstein, 1998; Myers *et al.*, 2000) to capture and prioritize substantial new flows of conservation investment (Dalton, 2000; Myers & Mittermeier, 2003). These schemes are outputs from analyses that are essentially biogeographical in nature, and they are having an immense influence in the organisation and prioritisation of conservation efforts (Jepson & Whittaker, 2002a, Myers & Mittermeier, 2003). As such they are perhaps the most prominent of recent conservation biogeographical developments: but many other approaches also warrant attention. Thus, in the following, we illustrate our case by brief reference to a wide range of biogeographical applications rather than providing an in-depth review of each. Even so, there are areas of conservation biogeography, which, for reasons of space, get little or no mention.

In climate change research, a mature debate has developed based on assessing how sensitive future climate scenarios are to starting assumptions and model parameters (e.g. Gerber *et al.*, 2004). In this, conservation biogeography lags some way behind. Indeed there appears to be a certain reluctance to entertain critical debate on the merits of particular schemes lest it detract policy makers from their implementation or lead to loss of public support. In illustration, critics of Conservation International's hotspots scheme (see, e.g. Humphries, 2001; Brummitt & Lughadha, 2003; Ovidia, 2003) have recently been labelled 'dissidents' by the scheme's originator (Myers & Mittermeier, 2003). Similarly, acknowledgement of the non-pristine nature of many rain forest areas stirs controversy in part because of the dilution in clarity of

the conservation message to policy makers (compare: Gillson & Willis, 2004; Hambler, 2004; Willis *et al.*, 2004a,b). As applies in climate change research, we must also have, as a discipline, the confidence to pursue critical analyses in order to improve the biogeographical advice being offered. A key objective of our paper is therefore to assess the sensitivity to assumptions inherent in the applications of Conservation Biogeography we review. In particular, we focus on (i) scale dependency; (ii) the Linnean and Wallacean shortfalls; (iii) model structure and parameterisation; and (iv) adequacy of theory. This is followed by a brief assessment of key research issues in the use of biogeography in developing and refining protected area planning frameworks.

WHAT IS CONSERVATION BIOGEOGRAPHY?

Herein we define Conservation Biogeography as '*the application of biogeographical principles, theories, and analyses, being those concerned with the distributional dynamics of taxa individually and collectively, to problems concerning the conservation of biodiversity*'. It is not a new area of scientific enquiry, but the conjunction of the words conservation and biogeography appears to have arisen very recently, in a meeting leading up to the first conference of the International Biogeography Society (held in 2003) and the nearest to a book of the title that we are aware of is *Applied Biogeography* (Spellerberg & Sawyer, 1999). As an applied and interdisciplinary science concerned with the conservation of nature, Conservation Biogeography can be seen as a sub-discipline of both Biogeography and Conservation Biology. We briefly consider the origins of these related endeavours in order of their emergence.

Biogeography is the study at all possible scales of analysis of the distribution of life across space, and how, through time, it has changed, within which a major concern has always been the distribution and dynamics of diversity, frequently codified in terms simply of numbers of species, or proportions of endemic species. The discipline has deep scientific roots, with some of the major themes already established as areas of enquiry by the early 1800s (Brown & Lomolino, 1998; Lomolino *et al.*, 2004).

By contrast, *nature conservation* can be thought of as a social movement working to develop or reassert certain values in society concerning the human–nature relationship (Jepson & Canney, 2001; Jepson & Whittaker, 2002b). The modern conservation movement emerged in the late 19th century in response to fundamental changes in world views concerning the human–nature relationship, emanating largely from elite society of the American East Coast and Western Europe (Jepson & Whittaker, 2002b). The movement was motivated both by a desire to preserve sites with special meaning for intellectual and aesthetic contemplation of nature and by acceptance that the human conquest of nature carries with it a moral responsibility to ensure the survival of threatened life forms. The movement gained new momentum in the second half of the 20th century when science further expanded understandings of the society–nature relationship (Frank *et al.*, 1999; Adams, 2004).

Motivated by, but distinct from the nature conservation movement, *conservation biology* is the name given for applied research

designed to inform management decisions concerning the conservation of biodiversity. As such, its roots lie largely within the mid-20th century: it gained huge momentum during the 1970s and early 1980s when it was formally identified as a sub-discipline, with dedicated journals and textbooks (e.g. Soulé, 1986; Primack, 2002). It is a large field, but if subdivided by scale of application, we might recognise the following subdivisions of relevant theory. First, the development and evaluation of biological theory spanning population biological and genetic process, and concerned with minimum viable populations, genetic erosion from small populations, competitive influence of invasive species, behavioural ecology, etc., i.e. concerned with processes in which biogeography is generally not prominent (e.g. see Primack, 2002). Second, theory concerning processes at the local-landscape scale, including the foundational influence of MacArthur & Wilson's dynamic (equilibrium) theory of island biogeography, the derivative Single Large or Several Small reserves (SLOSS) debate, habitat corridors, metapopulation theory, and nestedness (reviewed by Whittaker, 1998): i.e. bridging ecology and biogeography. Third, applications on a yet coarser scale in part are concerned with mapping and modelling biogeographic patterns and in part invoke historical biogeographic theory concerned with the distribution and explanation of geographical patterns in diversity, which can be referenced back to the founding fathers of the discipline of biogeography (Alfred Russel Wallace, Philip Sclater, etc.). We see such coarser scale work on the geography of nature as being unambiguously within the heartland of biogeography (cf. Lomolino *et al.*, 2004) and despite its undoubted importance within conservation science, we argue that it is here that the 'Cinderella' tag applies to conservation biogeography, and here where there is greatest need for critical attention to our science, and for greater interaction between those involved in theory and application (cf. Lourie & Vincent, 2004).

Conservation biogeography, the application of biogeography in conservation, is thus separable from the application of ecology and macroecology most clearly at coarser scales. Whilst the use of zoogeographic regions, areas of endemism, geographic patterns in species richness, or phylogeographic structure for conservation prioritisation purposes are readily identifiable as conservation biogeography, applications at increasingly fine spatial scales, for example focused on habitat corridors or metapopulation dynamics can be seen as simultaneously drawing from traditions in both ecology and biogeography. Similarly, macroecological analyses [referring to the analysis of the emergent statistical properties of ecological datasets (Brown, 1995)] may also be based on both 'ecological' traits (e.g. growth rates, propagule size, breeding system, body size) and 'biogeographical' traits (e.g. range size, region of origin). In illustration, efforts to develop explanatory and predictive models of invasiveness of non-native species have been made that mine both sets of traits, frequently finding a biogeographical signal in the resulting models (Dehnen-Schmutz, 2004; Pyšek *et al.*, 2004), indicative that such analyses draw from both ecological and biogeographical traditions within conservation science to varying degrees.

From this brief outline we highlight three points. First, the foundation of biogeography as a discipline substantially predates the emergence of conservation biology. Second, conservation biogeography forms an important, distinctive (but not entirely distinct) subset of conservation biology. Third, the motivating force for these scientific endeavours is a diverse social movement, representing varied values.

SOCIAL VALUES AND CONSERVATION BIOGEOGRAPHY

We are concerned in this article with the scientific underpinnings of conservation decision making. Yet it is important to recognise that such scientific guidance, and the language in which it is couched (Trudgill, 2001), is not value-free and that there is a debate to be had concerning what properties of nature we wish as a society to foster. Much of the scientific guidance and of current conservation practice assumes that this debate has a particular outcome, without paying much attention to the possible validity of alternative value systems (but see: Redford *et al.*, 2003). So, for example, Conservation International's hotspots (Myers *et al.*, 2000) delimit as priority regions areas that possess > 1.5% of global plant diversity uniquely within their bounds, and which have lost > 70% of their original habitat. In doing so, CI are necessarily placing higher value on those species that on a regional scale co-occur with many other range-restricted plant species, than they do on species occurring in other systems. Other value systems exist, such as those emphasising the importance of intact megafaunal assemblages, aesthetic and cultural significance of landscapes, ecosystem health or biotic integrity (cf. Callicott *et al.*, 1999; Redford *et al.*, 2003; Adams, 2004), and these value systems motivate conservation action in many nations, especially at local scales but also globally (Jepson & Canney, 2001, 2003; Trudgill, 2001).

The decision to adopt a particular set of values does not lie within the bounds of science, and although conservation scientists are well placed to contribute to debate, there is an important distinction between the processes leading to the adoption of a set of values, and the process of deriving the scientific guidelines to implement these values. So, whilst there may be pragmatic reasons to opt for a 'silver-bullet' approach (e.g. Myers *et al.*, 2000), conservation biogeographers should be in the business of providing alternative scenarios addressing differing end goals (cf. Williams *et al.*, 2000a; Dimitrakopoulos *et al.*, 2004). Thus, alongside the programme of exploring sensitivity to the more prosaic assumptions concerning data quality, modelling effects, etc., set out below, should be added sensitivity of outcomes to different societal objectives.

KEY ASSUMPTIONS AND SENSITIVITIES

(i) The Linnean and Wallacean shortfalls

Our knowledge of the overall biodiversity of the planet remains woefully inadequate, with estimates of global biodiversity ranging over one or possibly two orders of magnitude (Groombridge, 1992; Brown & Lomolino, 1998; Groombridge & Jenkins, 2000).

Much of the diversity we do know about has yet to be formally described and catalogued. In general, these problems — the so-called Linnean shortfall (Brown & Lomolino 1998) — appear to be of increasing severity as the organisms decrease in size and complexity, e.g. from vertebrate groups, to invertebrates, down to nematodes (e.g. see: Medellín & Soberón, 1999; Ødegaard *et al.*, 2000; Lamshead & Boucher, 2003). In so far as we do know our species, we also have, for many taxa, inadequate knowledge of their global, regional, and even local distributions, a problem that Lomolino (2004) has labelled the Wallacean shortfall. Many areas of the world remain seriously under-collected for most taxa, with the result that even for higher plants, reliable, systematic species range maps — the necessary basis for robust analyses of diversity patterns — are available only for a fraction of the earth's surface. Moreover, much of our distributional data and many of our compilations pertain to political geographical units (states) lacking biological meaning, which have gone their own ways historically in gathering botanical and zoological data, and which vary hugely in area: factors liable to produce serious artefacts when data are combined for analysis.

The following examples illustrate some of these problems, beginning with an esoteric choice: marine nematodes. Nematodes have been identified as a possibly hyper-diverse group, especially benthic nematodes in the deep sea (i.e. estimates of > 1 m species have been made). Yet, to date, very few marine nematodes have been described to species level, and these high values are derived using extrapolation techniques from local sampling. A recently collected transect spanning 3000 km of the abyssal plain of the north-central Pacific ocean indicated a regional richness of only a few hundred species (Lamshead & Boucher, 2003). Intriguingly, fully 71% of the species in the two northern stations of the transect were also collected from the (more species rich) southern stations. Not only is there a pronounced Linnean shortfall in marine nematodes, but the relationships between alpha, beta and gamma richness patterns now *appear* to be radically different between the shallow and deep seas, i.e. there is an equally large Wallacean shortfall, and initial assumptions now seen unfounded. On the basis of these and other recent data, Lamshead & Boucher (2003) suggest that a radical reassessment downwards of the global diversity of marine nematodes is necessary.

While the social and economic value placed on marine nematodes and their conservation may currently be limited, the same cannot be said of wild plants. The Atlas Florae Europaeae (AFE) is a project, launched in 1965 as a collaborative effort of European botanists, with the aim of mapping and providing taxonomic notes for the entire European flora. Some forty years on, twelve volumes have been published. Yet, as of 2003, the AFE was able to claim only that the maps cover families that include *more than 20%* (our emphasis) of the vascular plants of the European flora. Moreover, electronic versions of early maps have only recently become available. We are still a long way off being able to take full advantage of the collections residing in herbaria and museums, notwithstanding massive improvements in computer power, etc. (Wheeler *et al.*, 2004).

Nelson *et al.* (1990) provide a tropical botanical example in their critique of 'centres of richness and endemism' (CORE

areas) for the Brazilian Amazon. The validity of these patterns is critical to debates on the Quaternary history of the Amazon (e.g. Bush, 1994; Colinvaux *et al.*, 2001). Nelson *et al.* (1990) quantified collecting intensity within the herbarium collection at Manaus by recording the number of specimens of the virtually ubiquitous tree genus *Inga* per 1° grid cell. They found that vouchers of *Inga* varied from 0 to > 320 per cell, and that only one of the seven previously proposed Brazilian CORE areas was not a focus of collecting activity: in short, the biogeographic pattern is confounded by collecting intensity. Despite recent interest in artefactual effects in diversity gradient analyses (e.g. Diniz-Filho *et al.*, 2003; Colwell *et al.*, 2004), formal analyses of possible artefacts in collecting effort and data quality underpinning coarse-scale strategic conservation schemes appear to be rare (but see, e.g. Prinzing *et al.*, 2003). It would seem worthwhile to explore the sensitivity of such data and schemes to the problems inherent in the Wallacean shortfall.

(ii) Scale dependency

Spatial scale: extent and focus

There are numerous metrics of diversity, and they have been applied on widely varying scales, often inconsistently (Whittaker *et al.*, 2001). A crucial distinction is that between (a) the geographical extent of a study system, being the space over which observations are made, e.g. a hillside, a state, a continent; and (b) the grain (focus) of the data, being the contiguous area over which a single observation is made, or at which data are aggregated for analysis, e.g. a light trap, 1 ha plot, or latitude–longitude grid cell. Often the term scale, or spatial scale, is used to refer to both of these quite distinct properties of study systems, but they are not equivalent or substitutable (Palmer & White, 1994; Nekola & White, 1999; Whittaker *et al.*, 2001; Whittaker & Heegaard, 2003). This is shown by analyses using nested sets of grid cells that reveal different patterns of diversity by varying grain and holding extent constant (Stoms, 1994; Rahbek & Graves, 2000, 2001; Koleff & Gaston, 2002). Similarly, when scale (i.e. grain) is held constant, but geographic extent is varied, again different patterns can result (e.g. Hawkins *et al.*, 2003). The failure to control for scale (e.g. by holding area constant in analysis) and the confounding of grain and extent within the diversity literature has undoubtedly hindered progress in the development of theory. These scale issues have a clear relevance to the development of strategic conservation frameworks, in so far as they make use of, or are dependent upon, mapping diversity patterns (Williams *et al.*, 2000a; Redford *et al.*, 2003). This is shown by Lennon *et al.*'s (2001) analyses of British birds, in which spatial patterns of richness using a 10-km grain grid system were found to be statistically unrelated to those using a 90-km grain system: with coarsening scale the locations of the most species-rich quadrats moved north. This indicates that reserve selection criteria based on species distribution and diversity data may be sensitive to the scale of analysis employed. Relatively little work has been done on this problem, although it may have a strong influence (Stoms, 1994; Araújo, 2004).

Range restricted species — and thresholds of rarity

Rarity, as Darwin commented, is often a precursor to extinction. Rarity can mean that a species occurs at low density, and it can mean that a species occupies a small geographic range. Given these two forms of rarity (and there are others: Gaston, 1994) a species can be: (i) abundant and widespread; (ii) abundant but localised; (iii) low density but widespread; or (iv) low density and localised. It has long been known that a high proportion of species have relatively small geographic ranges, and few are widespread. Brown's (1995) graphical macroecological analyses of range size and density indicate that within taxonomically or ecologically similar species there tends to be a positive correlation between these two properties. This means that species occupying large ranges tend to be more abundant throughout those ranges than range-restricted species, suggesting the corners of the plot represented by conditions (ii) and (iii) to be very unusual. When examining whole faunas, such as the Breeding Bird Survey data for North American land birds, a lot more scatter is evident than within similar groups of species, but still the condition of 'abundant and localised' (i.e. ii) is extremely rare (Brown, 1995, Fig. 6.2; and see Gaston, 1994). It would therefore seem that conservation biogeographers are right to focus attention on range-restricted species as being *a priori* of conservation concern (Rosenfield, 2002).

Yet, what constitutes a small range, and how might the range size/abundance pattern vary in relation to biogeographic context (e.g. continental versus island archipelago contexts) or for taxa of differing body sizes? In the North American breeding bird survey data set analysed by Brown (1995), range size varies from c. 10,000 km² to over 10 million km² and fewer than 10 species have ranges < 100,000 km². By way of contrast, the land area of the Canary Islands is only approximately 7500 km² and that of the Hawaiian archipelago is 16,640 km². Assuming that the typical pattern of many species with small ranges exists within these essentially self-contained biogeographic areas, then many native species have tiny ranges, and even the most abundant species on these islands will have smaller ranges than the 'localised, low density' rarities of the North American data set. In conservation, a common threshold for defining range-restricted (sometimes 'local endemic') species is that the range size is < 50,000 km² (from Terborgh & Winter, 1983). On this basis, the entire endemic biota of island archipelagos such as Hawaii, Galapagos and the Canaries would be classed as of conservation concern. This would be unduly pessimistic. A simple illustration is provided by the case of the Tanimbar corella (*Cacatua goffini*) — a parrot species endemic to the Tanimbar islands (Indonesia), a group of 66 islands of a total land area of about 5400 km². It was initially listed as 'threatened' in 1989 on the basis of small global range and concern that it was being traded at a possibly unsustainable rate, but field survey on the largest island, Yamdena (3250 km²) subsequently produced a population estimate of 231,500 (± 33,000) for that island alone, suggesting that the initial categorisation had been unwarranted (Jepson *et al.*, 2001). That an island species with a global range one-tenth the size of the Terborgh & Winter (1983) threshold for range-restricted species can have a healthy

population size is good news. Of course, this may be a misleading example, and it must be balanced against the knowledge that, for example, about half of Hawaii's indigenous bird species have gone extinct since human colonization, and that population data indicate many island species to be seriously threatened (Whittaker, 1998).

The threshold of 50,000 km² has been widely adopted in conservation prioritisation analyses (e.g. Long *et al.*, 1996; Rodrigues *et al.*, 2004), and for particular taxa and contexts is a reasonable approximation (e.g. for freshwater fish species in North America, Rosenfield, 2002). In the IUCN red list criteria, attribution can default to range size if other data are lacking, in which case, the thresholds used are 100 km² (extent of occurrence) for critically endangered, 5000 km² for endangered, and 20,000 km² for vulnerable (version 2.3; www.redlist.org/info/categories_criteria1994.html). This three-point scale recognises that on average, threat increases incrementally as range size reduces. For those schemes employing a single range size, whether 50,000 km² or another, it would appear valuable to undertake analyses for different taxa and biogeographical contexts of the sensitivity of prioritisation analyses to the adoption of that threshold (Williams *et al.*, 2000a). Moreover, to refine the meaning of 'range-restricted' for conservation prioritisation, we need more empirical data to translate range size distributions into population estimates (c.f. www.birdlife.org/datazone) across a large sample of species for different contexts, e.g. mainland versus island systems.

Temporal scale

In conservation biogeography we are — or should be — concerned with both temporal and spatial scale dependency (Gillson & Willis, 2004). By analogy to the terms used in considering spatial scale, the study 'grain' in temporal analyses would refer to the interval between data points, and the 'extent' to the temporal depth of the analysis. Although fine resolution data often reveal oscillations hidden in coarse resolution assessments, typically, it is the sensitivity of forward projections to the length of the data series used that is of greatest concern in the present context. Conservationists aim to ensure the survival of species in the long term. Hence it is important to understand the temporal dynamics of biogeographical processes and whether short-term trends can be projected into the future (Gillson & Willis, 2004). Yet, the rapidity of contemporary changes such as habitat fragmentation is such that attempts typically have to be made to project far into the future on the basis either of snapshot data or of very short temporal series. There are many attendant difficulties in doing so, as for instance, the ecosystem dynamics of forest fragments may respond to forcing via subtle alterations to the population dynamics of the dominant organisms (e.g. forest trees) on decadal or multiple-decadal timescales (Bush & Whittaker, 1991; Whittaker, 1998; Willis *et al.*, 2004a).

A classic illustration both of genuine reasons for concern and of the uncertainty involved in projections is provided by the tropical moist forests of the Atlantic seaboard of Brazil, which have been reduced over the past few centuries to only an estimated 12% of their former cover. Simple species–area calculations, based

on island biogeography theory, predict about 50% extinctions. To date, none have been documented with certainty, although species-level assessments show many species to be IUCN listed as vulnerable, endangered or critically endangered based on range, or population estimates (see www.birdlife.org/datazone). Brooks and Balmford (1996) compare losses of birds projected using the species–area approach with those listed as ‘threatened’ and find congruence, i.e. they argue that the predictions are basically correct, but that there is a substantial lag between the habitat loss/fragmentation process and global extinction of the species. It should of course be recognised that species–area analyses based on island theory provides only a coarse, stochastic simulation of impacts of fragmentation, and the actual drivers of extinction may be structured, and in some instances avoidable by appropriate management. Conservation action in the Atlantic forests has likely already been and will continue to be crucial to staving off the predictions of the species–area models (Birdlife EBA factsheet 75, www.birdlife.org/datazone/ visited July 2004). This also means that in many cases it is impossible to distinguish between inadequacies of theory (reviewed in Whittaker, 1998) and successful implementation of conservation strategies.

Considering Quaternary-scale studies, it is difficult to obtain high precision data on past ecosystem dynamics and how they relate to environmental driving forces, particularly at a mechanistic level. Techniques such as pollen analysis offer the best resolution, and have greatly improved our understanding of responses to climatic forcing. In essence, systems respond highly individually, such that past community signatures exist for which there are no modern-day analogues (e.g. Bush, 1994, 2002). Yet, palaeoecologists still debate the respective roles of changing moisture regimes, temperature regimes and CO₂ concentrations in driving the changes (Bennett & Willis, 2000; Colinvaux *et al.*, 2001). There is also a considerable degree of uncertainty concerning the migrational lags evident in range adjustments to climate forcing. Long distance dispersal at low density is likely to be the

key to understanding such range shifts but is a difficult process to model. Recent work by Kullman (e.g. 1998) indicates that traditional pollen analytical techniques underestimate the ability of some temperate species to respond rapidly to climate warming events. Such insights, and others derived from phylogeography, demonstrating genetic legacies from the restriction and subsequent emergence of populations from refugial areas, can contribute considerably to an improved theoretical understanding of responses to climate forcing, and to the parameterisation of models forecasting future changes (Fig. 1; Willis & Whittaker, 2000; Bush, 2002; Schmitt & Krauss, 2004).

(iii) Effects of model structure and parameterisation

In this section, we focus on the sensitivity of conservation-biogeographical analyses to how we construct and parameterise our models. The taxonomic resolution at which we set priorities is one example. Endemism is usually considered in schemes such as Endemic Bird Areas (EBAs) (Long *et al.*, 1996) at a species level, but could be analysed at family, genus, species or subspecies levels, each implying a diminishing degree of taxonomic distinctiveness or evolutionary distance. All of the regional and/or global prioritisation schemes (as Table 1) that we are aware of operate at the species level. How might they change if conducted at the family level, or the subspecies level? Modelling of how spatial patterns of plant richness varies at species, genus and family levels suggests that whilst species and genus level patterns are closely related, shifting to the family level may produce significant differences (e.g. O’Brien *et al.*, 1998, 2000; Dimitrakopoulos *et al.*, 2004).

An illustration of the effects of adopting different modelling approaches is provided by da Silva *et al.*’s (2004) analyses of endemism in passerine birds of the Atlantic forests of eastern South America: a well-recognised biogeographical unit. The steps in their analysis were as follows: (a) define operational geographical units (OGU); (b) construct a data matrix; (c) perform

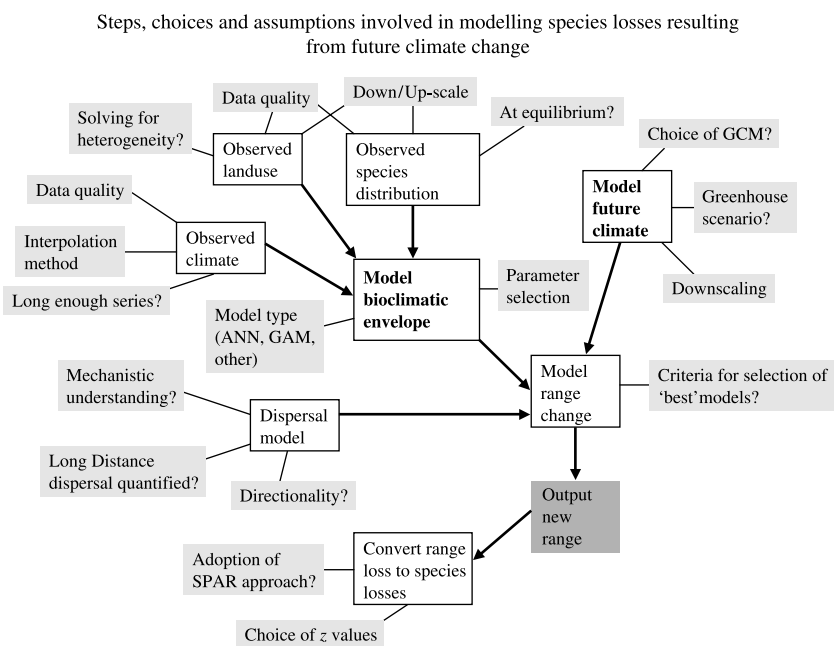


Figure 1 Some of the steps, choices and assumptions involved in modelling species losses resulting from future climate change using the bioclimatic envelope modelling approach (e.g. Pearson & Dawson, 2003; Thomas *et al.*, 2004; Thuiller *et al.*, 2004). Not all studies involve all elements, e.g. land-use data, or dispersal models, but these components are important for increased realism (Pearson & Dawson, 2004). Original.

Table 1 A typology of protected area planning frameworks of global remit. Biogeographical representation approaches set out to identify representative examples of ecosystem types identified using established biogeographical or ecological frameworks (e.g. Dasmann, 1972, 1973; Udvardy, 1975; Dinerstein *et al.*, 1995). In contrast to this largely zonal approach, hotspot approaches are azonal, and target places rich in species and under threat (e.g. Long *et al.*, 1996; Myers *et al.*, 2000). The Global 200 Ecoregions project combines elements of both hotspot and representation approaches (Olson & Dinerstein, 1998). The approach designated 'important areas' uses criteria such as numbers of wintering wildfowl congregating in the site, or importance of site as a stage in a migration route, to identify important areas for prioritisation (e.g. <http://www.birdlife.net/action/science/sites/> visited September 2004). Source: P. Jepson & R.J. Whittaker (unpublished)

	Global protected area planning frameworks		
	Representation	Hotspots	Important Areas
Basic idea	An example of each	Maximize number of species 'saved' given available resources	Select a suite of sites that together protect key attributes of concern
Questions arising	What are the units of nature? What do we add next?	Where are places rich in species and under threat?	What are the key attributes & how can they be assessed?
Parameters	Vegetation formations Faunal regions Ecoregions	Species richness Species endemism Rate of habitat loss % original habitat	Threatened species Endemic species Species assemblages Congregating species
Methods	% dissimilarity Controlling factors	Species counts Threat/diversity indexes	Application of varied criteria
Schemes	Biogeographic provinces WWF Ecoregions	Biodiversity Hotspots Endemic Bird Areas Global 200 Ecoregions	Important Bird Areas Key Biodiversity Areas

a parsimony analysis of the data matrix to produce an area cladogram; (d) delimit the OGU or groups of OGUs defined by at least two endemic species; and (e) map the species endemic to each OGU or groups of OGUs to delineate the boundaries of each area of endemism. OGUs can be outputs from previous schemes, e.g. ecoregions, biomes, provinces, or as in this case, grid cells (24 cells spanning 1°). Their analysis identified four areas of endemism (Pernambuco, central Bahia, coastal Bahia and, Serra do Mar) that exhibit some congruence with those identified for woody plants, bamboos, and swallowtail butterflies, suggesting that they may have some generality. However, as they also point out, they contrast with previous analyses of vertebrate data, in identifying varying numbers of areas of endemism, with incomplete overlap with their own. Whilst the differences arise in part from improvements in data, they in large part reflect model effects. In particular, their use of Parsimony Analysis of Endemism is controversial in that the methods are subject to heated dispute amongst historical biogeographers (e.g. see Brooks & van Veller, 2003; Ebach *et al.*, 2003). The degree of difference in the outputs between da Silva *et al.*'s analyses and Stattersfield *et al.*'s revised (1998, and see Long *et al.*, 1996) scheme is not huge but it is noteworthy in that the latter's Endemic Bird Areas approach has already provided a key strategic planning tool for the deployment regionally and globally of the conservation advocacy efforts of Birdlife International. There would again seem to be scope for further analyses of the sensitivity of this form of 'hotspot' mapping outcome to model assumptions, and this may require

biogeographers to adopt flexible and inclusive approaches to their work. Whilst the goal for an international NGO may appropriately be the production of a single map for conservation prioritisation (Redford *et al.*, 2003), the broader conservation biogeography community should be concerned with providing sets of alternative maps, based on varying parameters and choices.

A key distinction within spatial diversity analyses is that between richness and endemism, i.e. between the number of species per unit area and the number of local/regional endemic species per unit area. Areas rich in (restricted-range) endemics are often also species rich, but there is high variability at regional scales (Williams *et al.*, 2000a), and patterns in richness and endemism are not necessarily positively related (see maps in Huntley, 1996). Whittaker *et al.* (2001, 2003) argue that explaining patterns of endemism requires theories focussing on evolution and historical contingencies, whilst species richness patterns can often be related to contemporary ecological processes and controls. This decoupling is of more than merely theoretical interest, as prioritisation schemes based on maximising richness may produce different outcomes from ones based on maximising numbers of endemics (Williams *et al.*, 2000a).

This is illustrated by Dimitrakopoulos *et al.* (2004) who, in essence, provide a sensitivity analysis for prioritising plant diversity in Crete at species, genus and family levels using a grid of cells each of 8.25 km² (Fig. 2). They used hotspot analysis and complementarity algorithms to define priority areas for conservation to compare with the recently designated Natura 2000 Special Areas of Conservation (SACs) in Europe. The Natura

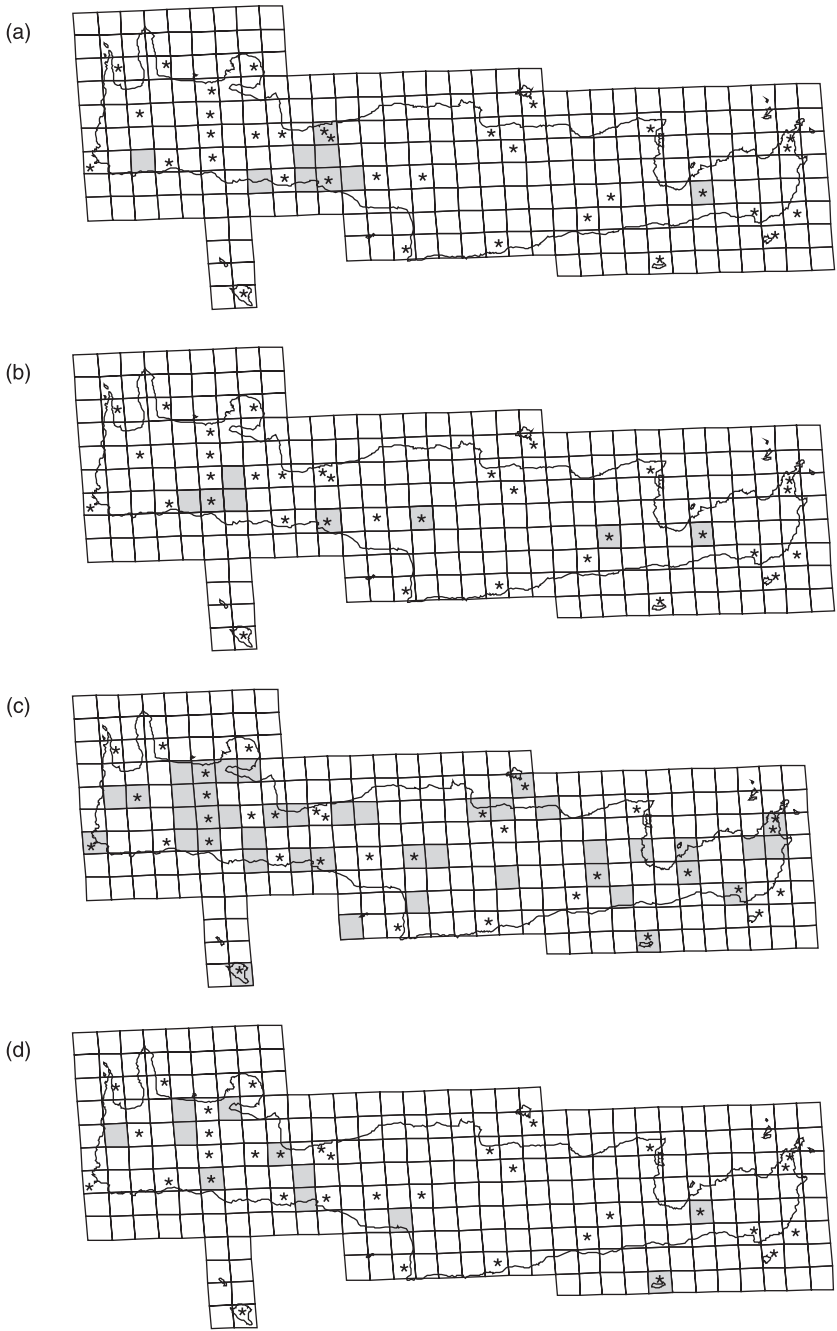
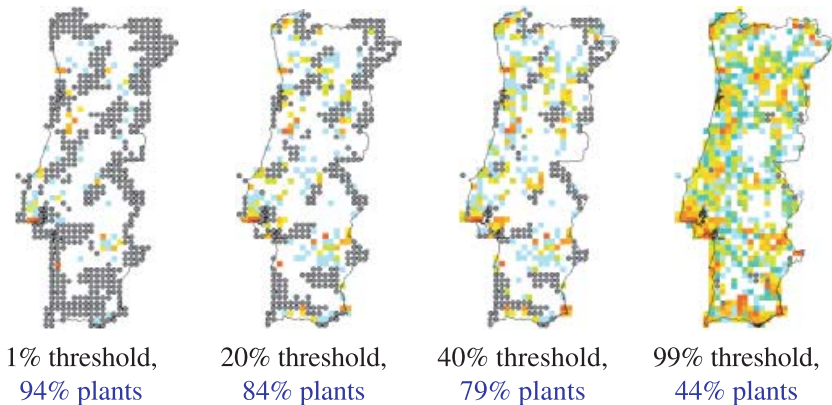


Figure 2 Alternative maps of potential conservation prioritisation of plants in Crete, based on 162 grid cells of 8.25 km². Locations of: (a) species richness hotspots; (b) species threatspots and endemic hotspots; (c) grid cells chosen to represent all genera at least once; and (d) grid cells chosen to represent all families at least once. The asterisks indicate the Natura 2000 Special Areas of Conservation. (From Dimitrakopoulos *et al.*, 2004, Figs 1 and 2). See text for further details.

2000 network was based on an area-selection strategy mostly concerned with representativeness, quality of habitat, size, density of listed species, and the degree of their isolation. In their comparative analysis, Dimitrakopoulos *et al.* scored each cell for: species richness, a vulnerability index (based on IUCN listings), a taxonomic distinctiveness index (reflecting proportionality of species-genus-family membership), a rarity index (reflecting species of restricted range within Crete), and endemism (i.e. island endemics). When these differing indices are used to identify hotspot areas (i.e. the top 5% of cells) and complementary sets (i.e. the minimum number of cells containing all target taxa), they produce quite varied outcomes (Fig. 2). For instance, the

spatial overlap between rarity hotspots, endemic hotspots and threatspots is only about 33%, whilst that between the complementary sets calculated for all species and the various categories of hotspot is less than 9%. In addition, the congruence with the Natura 2000 sites is also low — these sites cover a substantial area, located in 32 grid cells, but the overlap between them and the various hotspot categories is at best only 14%. This analysis indicates that Natura 2000 sites in Crete do not provide a particularly good representation of the plant diversity of the island. The analysis also shows that model effects, viz: (a) hotspot versus complementarity algorithms; (b) taxonomic resolution; and (c) priority given to richness, taxonomic distinctiveness, and rarity,

Figure 3 Sensitivity to thresholds in modelling representation in Protected Areas. Coloured cells show species richness (maximum values in red) of plant species not represented in reserves using 10×10 km grid cells (for mainland Portugal). A cell is switched on as reserved dependent on how much of its area is covered by a reserve, using thresholds varying from 1% up to 99%. Grey cells are those that have at least some reserved area within them (figure modified from Araújo, 2004, Fig. 2; reproduced with permission from Elsevier).



provide for a highly diverse range of conservation solutions. Such model effects are likely to be typical of reserve selection analyses (e.g. Fig. 3). A further problem that has been identified in analyses of this sort is that there is often a multiplicity of different but equally efficient complementarity solutions, meaning that comparisons such as that carried out for Crete should be based on multiple runs to ensure that the differences resulting are robust (e.g. Gaston *et al.*, 2001; Hopkinson *et al.*, 2001; Araújo *et al.*, 2005).

There is now a substantial body of work showing variability of area selection outcomes as a function of starting assumptions and goals (e.g. Pressey & Nicholls, 1989; Williams *et al.*, 1996, 2000a, 2000b; Rodrigues *et al.*, 1999; Andelman & Fagan, 2000; Dimitrakopoulos *et al.*, 2004). However, these studies typically concern simple problems at a regional scale, ignoring issues of range dynamism, and being restricted to single taxa. Whilst some studies have improved on these static approaches (e.g. Araújo & Williams, 2000; Araújo *et al.*, 2002a,b; Cabeza, 2003; Cabeza *et al.*, 2004), if we begin to consider more sophisticated problems, such as the conservation implications of climate change, with all the associated uncertainties, then the various model effects multiply (Fig. 1; Araújo *et al.*, 2004a; Meir *et al.*, 2004; Williams *et al.*, 2005). The use of so-called bioclimate envelope models to capture the relationship between species distributions and climate space and thereby to model future responses to climate change has advanced considerably in the last few years. Yet, the sensitivity to key assumptions is such that the resulting bioclimate envelope modelling projections are so uncertain as to effectively compromise their practical value (compare Buckley & Roughgarden, 2004; Thomas *et al.*, 2004; Thuiller *et al.*, 2004) notwithstanding the wider impact they may have (Ladle *et al.*, 2004; Hannah & Phillips, 2004). These models should be seen as providing merely interesting 'what if' scenarios, until such time as we find ways of assessing model variability and reliability quantitatively (Hannah *et al.*, 2002; Pearson & Dawson, 2003, 2004).

(iv) Adequacy of theory

In addition to practical issues concerning e.g. finding the most efficient tree building or complementarity algorithms, it is also important to consider the adequacy of biogeographic theory. Whilst this theme is only partially separable from the foregoing sections, it is important to focus explicitly on some of the deeper

questions concerning the paradigmatic structures within which conservation biogeography has so far been constructed. For instance, in respect of spatial scale, it has long been appreciated that species richness of otherwise equivalent sample areas increases as larger areas are sampled. Thus comparative analyses of richness — whether exploring causation in species diversity or assessing conservation importance — which fail to hold area effectively constant, are fatally compromised (Whittaker *et al.*, 2001; Brummitt & Lughadha, 2003; Ovadia, 2003). One reason they continue to feature in the literature is that insufficient efforts have been made to develop diversity theory structured with respect to scale (Whittaker *et al.*, 2001, 2003; Willis & Whittaker, 2002; Rosenzweig, 2003; Whittaker, 2004).

In respect of temporal perspectives, despite a number of calls for change, a paradigmatic structure persists within conservation that the environment has two 'states': pre- and post-anthropogenic impact. Prior to anthropogenic impact the ecosystems is viewed as an undisturbed natural system in equilibrium with the environment: it is 'pristine' and change is slow. In contrast, the post-anthropogenic period is seen as a time of rapid change, where a threshold is exceeded and the environment irrevocably altered for the worse. Yet there are now numerous studies to indicate that this structure is far too simplistic. For instance, some of the systems associated with the labels 'pristine' and 'fragile' turn out to have recovered from past intensive human use (Willis *et al.*, 2004a,b). The use of such value-laden terms is part and parcel of this two-state worldview (cf. Stott, 1998; Trudgill, 2001), and it is a paradigm we surely need to break away from in recognition of the capacity of biogeographical phenomena to be variously equilibrial and non-equilibrial dependent on the properties under scrutiny, the geographical context, and the spatial and temporal scales of the assessment (as Whittaker, 2004).

One prominent contribution of biogeography to conservation biology has been the use of island theory, in which the dynamic, equilibrium theory of MacArthur & Wilson (1967) has been seminal. We take this body of theory in illustration of the importance of improved theoretical foundations. In the early 1970s, Diamond (1975) and others set out a theoretical framework for fragmentation research derived from MacArthur–Wilson theory, which has spawned a host of studies of species area relationships (SPARs) for terrestrial 'habitat islands'. The premise is that habitat fragmentation will produce predictable patterns of species

loss as previously equilibrated patches become 'supersaturated' and thereafter 'relax', i.e. shed species. Diamond drew on supporting quantitative evidence for relaxation coming largely from 'land-bridge islands', the assumption being that prior to sea level rise at the start of the Holocene, these islands would have been connected to the mainland, and would have shared close to the full quota of species now present on the mainland. The discrepancy between this assumed starting value and that derived from species-area plots for 'control' areas is taken to represent the number of extinctions, with the speed of equilibration being seen as an inverse function of area. The possibilities that the observed discrepancies reflect the influence of variables other than area and isolation, or that biotas may not initially be in the assumed equilibrium richness state prior to fragmentation (Boecklen & Gotelli, 1984; Boecklen, 1986) were recognized but downplayed. Diamond made a number of fairly bold statements about our ability to predict not only total numbers of losses (the oft-cited 50% species remaining in 10% of the area figure) but also rates of losses. Then, as now, such predictions appear to be derived largely from inferences based on studies of actual islands, and of the form of SPARs (e.g. Rosenzweig, 1995, 2003) rather than on studies of recorded losses from fragmented habitats within large landmasses (but see Stouffer & Bierregaard, 1996).

It is disappointing that we still know so little about the power and timescale of 'species relaxation'. There have paradoxically been many studies of fragmentation, but remarkably few appear to have had 'before' and 'after' data or have undertaken repeat surveys of the same fragments over a lengthy period (but see Honnay *et al.*, 1999; Gonzalez, 2000; Bierregaard *et al.*, 2001). As a result, inferences have to be made based on the use of the species-area relationship, typically assuming: a fixed z value (slope) of 0.25 (e.g. Brooks *et al.*, 2002), that the system was essentially equilibrated prior to fragmentation, and that the properties of the matrix habitats can be ignored. Each of these assumptions is problematic (Whittaker, 1998; Watson *et al.*, 2005).

An important contribution to our understanding of SPARs is provided by Rosenzweig (1995, 2003), who demonstrated the importance of separating out different categories of curve (and see Scheiner, 2003, 2004; Gray *et al.*, 2004a,b). First, we may recognize and discount species-accumulation or collectors curves (Gray *et al.*, 2004b), which describe the increase in total number of species with increasing collection effort within an area. Rosenzweig recognizes three scales of 'true' species-area curves (whereby number of species for each area is plotted against area), which he terms the sample-area, archipelagic and interprovincial. Respectively, these are (i) sample-area: constructed from considering different sized (non-nested) samples from within non-isolated habitat within the same region; (ii) archipelagic: from islands of an archipelago; and (iii) interprovincial: constructed from all species found in separate biological provinces, i.e. more or less self-contained regions whose species are predominantly native in origin. Rosenzweig argues that the z -values (slopes of the log-richness-log-area relationship) vary systematically between these three forms, (i) sample-area, typically between 0.1 and 0.2; (ii) archipelagic, typically between 0.25 and 0.55; (iii) interprovincial, 0.6–0.9. If these ranges are indeed typical, then they have

profound importance for understanding the eventual impact of fragmentation on species losses, just as was suggested by MacArthur & Wilson (1967). In other words, as systems move from the sample-area to archipelagic curve they should shed species, and should do so at a predictable rate.

Unfortunately, island theory does not tell us how species should be distributed across a system of fragments, and this is crucial to the issue of whether it is better to advocate one very large reserve, or several smaller ones of the same total area. To some extent, Diamond himself acknowledged this when he wrote 'separate reserves in an inhomogeneous region may each favour the survival of a different group of species; and ... even in a homogeneous region, separate reserves may save more species of a set of vicariant similar species, one of which would ultimately exclude the others from a single reserve' (Diamond, 1975). If we take two extremes, systems could be either perfectly nested, or perfectly non-nested. If nested, it means that each smaller set of species is a perfect subset of the next larger: in which case the total number of species held by the system of fragments is the number held in the largest (richest) patch. If the fragment system is perfectly non-nested, then the number held in the system as a whole is the sum of the number held in each patch, as each contains unique species (Fig. 4). Empirical work to date indicates that most systems tend significantly towards being nested, but are not perfectly nested (Whittaker, 1998). But, how sensitive are these observations, of SPAR z -values and of compositional structure, to the scale of our system, i.e. to the grain and extent of the data? As fragments are

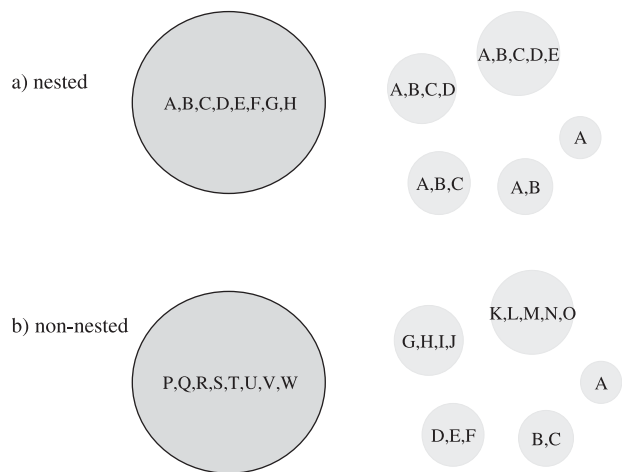


Figure 4 A variant on the theme of the design principles for nature reserves, originally derived from consideration of island theory by Diamond (1975) and others. Here we posit a choice between a single large reserve and a network of smaller reserves of approximately the same total area. In the perfectly nested system, the largest reserve contains all the species in the reserve network. In the perfectly non-nested system, the set of smaller reserves contains more species than the largest reserve and no species in common with it. Empirical data tend to support nestedness as a general property of small island/habitat island data sets sampled from within a landscape or small region. The degree of nestedness must diminish if islands/habitat islands from across larger areas, or distinctive biogeographical areas are considered.

considered across a wider area, encompassing more diverse microenvironments and more biogeographic history, so we capture more beta diversity, and nestedness must diminish in a habitat island data set. Thus, the answer to the SLOSS debate can be expected to change from an emphasis on large reserves to an emphasis on many, comparatively smaller reserves, as the grain and extent increase above the local-landscape scale.

Moreover, it has recently been argued that the approach to model fitting for SPARs should be based on an updated consideration of ecology rather than statistics, i.e. that we should examine the fit of theoretical (mechanistic) models against empirical data sets rather than setting out to find the best straight-line fit through the data (Tjørve, 2003). Lomolino (2000) has also questioned the approach of using data transformation in search of the best linear fit. He argues that there may be good ecological reasons to posit more complex scale-dependent relationships, and that untransformed SPARs should exhibit a sigmoidal form, with a phase across low values of area where species numbers scarcely increase, followed by a rapid increase with area and a subsequent flattening as the number of species approaches the richness of the species pool. The existence of a 'small island' effect appears well established (Lomolino 2000, 2002; Lomolino & Weiser, 2001), and thus must have some influence on z -values in standard linear SPAR regressions, but Williamson *et al.* (2001, 2002) contend that there is no evidence of an upper asymptote. It is noteworthy that the form and biological meaning of SPARs remains the subject of so much debate and confusion. One important reason is that empirical data sets each have their own unique combination of variation in contributory environmental variables (e.g. area, elevation, climate, habitat type, isolation, disturbance histories, etc.). Each of which has relevance, but not necessary significantly so over all scales within the empirical data gathered. Perhaps unsurprisingly, few SPAR analyses have attempted to tackle such threshold responses in respect of the complex array of potentially important, interacting variables. It has thus proven difficult to identify general patterns, and to develop general models through this approach.

Yet, numerous habitat island data sets have been collected, and so what is needed is not necessarily new field efforts, but more concerted efforts in analysis and synthesis, to tease out the scale sensitivity of habitat island data sets, particularly, the form of their SPARs, and their compositional structure, and how these responses vary between different higher taxa (e.g. butterflies, all invertebrates, higher plants, birds). Some theoreticians, notably Rosenzweig (2003), see dire implications in the continued process of ecosystem fragmentation and area reduction as systems move from samples to archipelagic to interprovincial SPAR forms. Yet, it is also important to recognise that whilst on a global scale biodiversity is suffering attrition (i.e. species are going extinct at well above background rates), at local and regional scales, patterns of change are quite variable. The introduction of non-native species and alterations of habitat typically result in the loss of particular sets of species at the local scale, yet at the regional scale — and sometimes locally also — the net effect may commonly be increases in species richness (McKinney, 2002; Sax *et al.*, 2002; Sax & Gaines, 2003). How can such observations be reconciled?

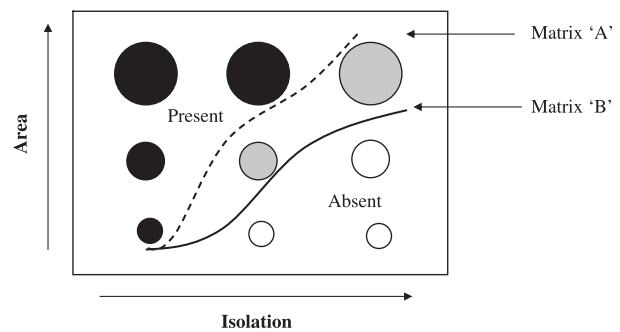


Figure 5 Insular distribution of a focal species (dark symbols indicate presence, open circles indicate absence), highlighting the possible effect of matrix properties on the presence of a species. The grey remnants and dashed line indicate that a species would inhabit these remnants when in a landscape with matrix composition 'A' but would not in matrix composition 'B'. From Watson (2004), after Lomolino (2000).

Perhaps, the whole paradigm of viewing habitat islands and reserves as islands has become part of the problem? Applied biogeographers have been so focussed on the fragments that they have paid insufficient attention to studying and developing theory encompassing the matrix. In his original 1975 paper Diamond noted other ecological features that influence the likelihood of persistence in reserves of different sizes, and captured some of this signal by the use of 'incidence functions' — a static analysis of the distribution of a species across a system of isolates. Recent work by Watson (2004; Watson *et al.*, 2005) has demonstrated that at least in some ecological contexts, matrix effects can be pronounced. Analyses of incidence of 27 woodland bird species in three landscapes from the Canberra area of the Australian Capital Territory, in relation both to area and isolation show a remarkably varied response not just between species, but between populations of the same species in different landscapes; where the principal apparent difference is not in properties of the woodland habitat islands, but in the characteristics of the matrix habitats (defined as urban, peri-urban, and rural) that contain the habitat islands (Figs 5 & 6). Although the premises from which we arrive at these conclusions may differ, we are in agreement with Rosenzweig (2003) and others (e.g. Renjifo, 2001; Lindenmayer & Franklin, 2002; Wethered & Lawes, 2002) in arguing that greater attention needs to be given to developing guidelines for so-called 'extensive' conservation efforts encompassing processes across whole landscapes — i.e., conservation within the matrix in which the reserves are embedded.

PROTECTED AREA PLANNING FRAMEWORKS — MAPPING PRESENT AND FUTURE BIOGEOGRAPHIES

A typology of frameworks with particular reference to the global scale

It is important to recognise that in practice, the designation of protected areas has been and will continue to be influenced by

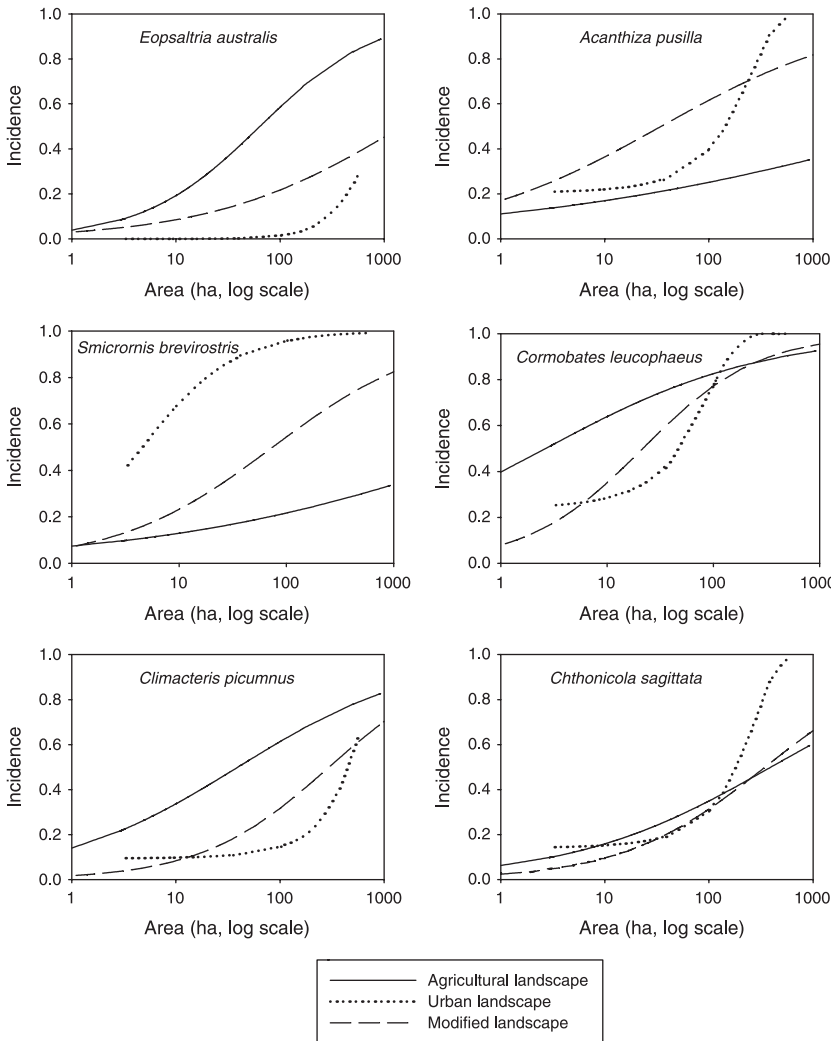


Figure 6 Incidence curves for six area-sensitive woodland species in different landscape matrices in the ACT region of southeastern Australia. The three woodland landscapes surveyed were: agricultural ($n = 55$ fragments), modified (peri-urban) ($n = 42$) and urban ($n = 30$). Incidence functions were developed using the results of a logistic regression based on the presence/absence of each species in woodland remnants in each landscape. From Watson (2004).

diverse and complex environmental, socio-economic and political factors (e.g. Sutherland, 1998; Jepson & Whittaker, 2002b). But in the following account, in the interests of simplification, we focus exclusively on the scientific principles underpinning the designation of protected areas.

The concept that the world is a patchwork of regions differing in their biological makeup has profoundly influenced how humanity perceives and interacts with the natural world. The concept of biological regions emerged as a result of European expansion in the tropics from the 16th century onwards and the desire to understand the diversity, richness and patterns of nature for religious, intellectual and economic purposes (Lomolino *et al.*, 2004). The realisation that nature differed in different parts of the world, and the subsequent spatial representations of these differences, played an important role in the planning and execution of the European colonial endeavour, the creation of national identities, and the development of international tourism among other things. Maps play an important role in the communication of biogeographic theory and are powerful tools within conservation biogeography (cf. Dalton, 2000; Myers & Mittermeier, 2003). But, maps are only a symbolic representation of nature

(Demeritt, 2001), and the choice of criteria and variables used to create the maps will be strongly influenced by what the creators of the map value (Williams *et al.*, 2000a).

In the 1960s there was widespread support within the conservation community for the goal of establishing a worldwide network of natural reserves encompassing representative areas of the world's ecosystems. Under the aegis of the IUCN, Dasmann (1972, 1973) and Udvardy (1975) put this 'biogeographic representation principle' into practice, by extending and combining earlier maps of faunal regions (Wallace) and vegetation zones (Clements) to create a nested hierarchy of biological regions (Table 1, Jepson & Whittaker, 2002a). Their work is foundational within conservation biogeography and provided the framework for a massive and rapid expansion of protected areas globally.

The Dasmann–Udvardy framework subdivides the globe into faunal regions (biotic realms) within which a biome classification system is applied, with biotic provinces delineated by subdividing a physiognomically defined climax vegetation type on the basis of a distinctive fauna. Areas with less than 65% of their species in common are delimited as separate faunal provinces, and this essentially zonal scheme is afforded by the recognition of

azonal features such as high mountains and mountainous islands. As originally developed, the approach was confined to bird and mammal data and to a coarse scale of application, but it was subsequently refined for use at a finer scale, by using the same algorithm for smaller geographical units (Mackinnon & Wind, 1981; Mackinnon & Mackinnon, 1986a,b; Jepson & Whittaker, 2002a). This scheme provides a transparent methodology with a clearly defined purpose, and in principle the analysis can be repeated to assess the implications of, for instance, using updated distributional data, a different system of biogeographic regions (cf. Cox, 2001), or threshold similarity value.

Since the development of the biogeographic regions approach, the tools for biogeographic research have undergone a radical transformation, as computerised databases and advanced spatial analytical approaches have been developed. Whilst the Dasmann–Udvardy approach remains an important foundational scheme at a global scale (Table 1), it has in practical terms been superseded at this scale by other global schemes developed and promoted by major conservation NGOs, whilst within regions a far greater array of approaches have been developed both by NGOs and other actors from the scientific community (e.g. Redford *et al.*, 2003). In Table 1 we identify the WWF Ecoregions scheme as a prominent global scheme based on the principle of biogeographic representation (e.g. Dinerstein *et al.*, 1995). It incorporates data on biogeography, habitat type and elevation to identify biogeographic units at a finer scale than the original Dasmann–Udvardy framework. The approach aims to meet the goals of representation and also to draw up natural units within which ecological flows and linking processes are maintained. In this way, the approach combines both compositionalist and functionalist perspectives (as Callicott *et al.*, 1999; Williams & Araújo, 2000, 2002). The WWF Ecoregions approach, specifically as applied within Indonesia, has been criticised by Jepson & Whittaker (2002a) for a variety of reasons, including data deficiencies and a lack of transparency as to the criteria involved in fine-scale designations. No schemes are entirely free of such problems, and Wikramanayake *et al.* (2002) provide a defence of the approach in an equally forthright reply. The scheme's proponents are of course driven by the heavy responsibility of getting on with the job of putting theory into practice, and effecting conservation actions on the ground. But, it would be naïve to think of any such map as being the final say in land-use planning and designation, as such battles have to be constantly re-fought and occasionally land abandonment provides new opportunities for ecological restoration and/or for inclusion of new areas into protected area networks (cf. Meir *et al.*, 2004). Magnusson (2004) argues that as ecoregion approaches are being heavily promoted, more rigorous tests of their delineation are urgently needed. He was writing about an attempt to test the validity of Bailey's foundational ecoregions scheme, but the same case can be made for the WWF scheme. Magnusson suggests a simple approach involving looking for natural breaks in species distributions across ecoregion boundaries, and a more sophisticated approach to the problem is illustrated by Williams (1996) and Williams *et al.* (1999).

To improve further on the alternative representation frameworks available requires several components. First, the criteria of

the scheme must be transparent and explicit. Second, the data on which the frameworks are built must be available and of a quality sufficient to the task, involving both biogeographical data and environmental data. Third, schemes once developed should be subject to further, independent tests of their efficiency and robustness (as e.g. Stoms, 1994; Williams *et al.*, 1999). In practice, the broad framework for biogeographic representation is generally agreed at the global scale (although, see Cox, 2001) and it is arguably at the meso-scale that improvements in data quality might produce significant alterations in the maps and adjustments in conservation efforts.

An alternative approach to reliance on biogeographic data *sensu stricto* was formalised by Faith & Walker (1996a,b), who based their approach on the correspondence between increasing numbers of (and/or increasing difference between) environmental domains and increased biodiversity. They noted that sampling environmental pattern, or compositional variation within one indicator group, would predict compositional variation within other groups if they spanned the entire range of habitats or environments available. Hence, sampling environmental pattern (or assemblage pattern) itself would be an alternative to selecting areas using species distribution data directly. Whilst this approach has some merits, its effectiveness in achieving pre-determined goals has yet to be consistently demonstrated (compare Faith and Walker, 1996a,b; Ferrier & Watson, 1997; Araújo *et al.*, 2001, 2004b). For example, Araújo *et al.* (2001) showed that European plants exhibited consistent non-random positive patterns of representation with conservation areas selected to maximise pattern variation among environmental domains, but that terrestrial vertebrates (especially reptiles and amphibians) were consistently under-represented with this approach. They argued that the degree of success of environmental-diversity strategies would be contingent on the contribution of historical biogeography shaping current distributions. According to this view, taxa with poor dispersal abilities (e.g. reptiles and amphibians) would be in clear disadvantage compared with those of good dispersal abilities (e.g. plants), which would more easily achieve conditions of quasi-equilibrium with current environmental conditions, and hence would be better predicted by environmental-based surrogates. Although evidence of the ability of environmental- and assemblage-based models to represent biodiversity at a rate higher than expected by chance is currently lacking (Araújo *et al.*, 2003), the approach is still strongly advocated by its proponents (e.g. Faith, 2003; Faith *et al.*, 2004). This is one example where conservation values, epistemology, theories of equilibrium in biogeography and numerical ecological techniques are intermingled in a complex but possibly important debate within Conservation Biogeography.

Hotspot approaches at the global scale contrast with biogeographical representation approaches by focusing on the richness and endemism of areas combined with a measure of the threat to biodiversity (Table 1). There are a number of prominent global schemes, including: the IUCN–WWF Centres of Plant Diversity, Birdlife International's Endemic Bird Areas (e.g. Long *et al.*, 1996; Stattersfield *et al.*, 1998), and Conservation International's (CI) hotspots (Myers *et al.*, 2000). Applications of the hotspots

approach are based, partly through necessity, on a limited array of taxa. For instance, the 25 CI hotspots are delimited solely on the basis of plant endemism and habitat conversion statistics. Myers *et al.* (2000) claim that the hotspots hold 44% of the world's plant species and 35% of the vertebrates in 12% of the land area of the earth. These taxa, however, represent a relatively small proportion of the species on earth, and it remains to be established what proportion of, for example, insects, are found within these areas. The areas delimited are also far too coarse, of themselves, to guide issues such as reserve placements. Rather they provide a global 'cookie cutter' of large areas deemed most deserving of conservation funding and attention. The approach has been remarkably successful in terms of fund raising, and if successful in implementation could make a significant contribution to reducing global biodiversity loss (Myers & Mittermeier, 2003).

The CI hotspots approach can be criticised on several grounds, including: (i) that it serves only a limited set of values (Jepson & Canney, 2001); (ii) that it sends out a powerful if entirely unintentional signal that biodiverse areas excluded from the list of hotspots do not matter in conservation terms (Bates & Demos, 2001); (iii) that it is a very coarse-resolution and simplistic analysis (Mace *et al.*, 2000); and (iv) that there seems to be no underlying base map, and certainly nothing approaching an equal-area grid cell system is involved, so that the basis for delimiting the boundaries of the areas selected appears essentially arbitrary. Moreover, in examining the applicability of the approach to the marine realm, Hughes *et al.* (2002) find that first, richness peaks do not coincide with centres of high endemism in Indo-Pacific corals and reef fishes, and second, that fish and coral endemism patterns are at variance with one another. They therefore argue against marine prioritisation by 'hotspots', instead calling for a focus on preserving connectivity and genetic diversity of widely dispersed species combined with intensive protection of quite localised areas of high endemism.

Criticisms have also been levelled at the way in which CI's 25 selected terrestrial hotspots have been ranked internally (Brummitt & Lughadha, 2003; Oviada, 2003), with Brummitt & Lughadha correctly arguing that the use of unscaled species-area ratios to select the 'hottest hotspots' is inappropriate. Myers & Mittermeier (2003) sidestep the scientific criticism in their response to Brummitt & Lughadha (2003), pointing to the urgency of action for conservation, the \$750 m raised in support funds for CI's hotspots scheme, and expressing frustration at the slowness of the scientific community to engage with their approach. The tension between the priorities of major NGOs and academic debate is understandable. The point of our listing the above criticisms of the WWF Ecoregions and CI hotspots programmes is not to undermine them as a basis for taking conservation action now, but to encourage an ongoing effort from conservation biogeographers to update, revise and test protected area planning frameworks at global and also regional scales. We see this as valuable because first, the broader goals of nature conservation are such that we need alternative sets of maps, capturing and representing different value sets, and second, because as our data, theory, and models improve, we can refine our planning frameworks to bet-

ter serve these goals (cf. Mace *et al.*, 2000; Williams *et al.*, 2000a; Rodrigues *et al.*, 2004). Moreover, as such large sums and efforts are involved, it is surely crucial that we provide the checks and balances to ensure that the resources are deployed effectively, and one part of this is about a continuing process of reviewing the scientific basis (Meir *et al.*, 2004).

To complete our typology of global protected area approaches (Table 1), we have designated a third type of approach — 'important areas' — as being distinct from representation and hotspot approaches. As exemplified by Birdlife International's Important Bird Areas (IBAs) scheme, important areas are key sites for conservation, small enough to be conserved in their entirety and often already part of a protected-area network. The stated criteria for selection of IBA sites are that they do one or more of the following things: (i) they hold significant numbers of one or more globally threatened species; (ii) they are one of a set of sites that together hold a suite of restricted-range species or biome-restricted species; and (iii) they have exceptionally large numbers of migratory or congregatory species (<http://www.birdlife.net/action/science/sites/> visited September 2004). The scheme provides a fine-scale network of sites, below the level of resolution of Birdlife's Endemic Bird Areas approach: for instance there are some 4000 IBA sites in Europe alone, in contrast to 218 EBAs globally.

In moving from the global to the regional scale of application, it is clear that there are numerous approaches to mapping and prioritising putative or existing protected areas (e.g. Pressey & Nicholls, 1989; Margules & Pressey, 2000; Williams *et al.*, 2000b; Cabeza & Moilanen, 2001; Williams & Araújo, 2002; Dimitrakopoulos *et al.*, 2004). Typically these approaches take grid-cell based species range data and use reiterative computer algorithms to select complementary sets of cells that achieve a predetermined goal. These approaches have the advantage of making goals, values and priorities explicit before area priorities are defined. They are quantitative, repeatable and ensure that efficient and effective solutions are obtained for a set of pre-selected goals and data (Williams *et al.*, 2000a). Unfortunately, they are also very data-hungry and highly sensitive to data quality (Flather *et al.*, 1997; Freitag *et al.*, 1998; Araújo, 2004; Araújo *et al.*, 2004b). Hence, quantitative 'gap analyses' have until very recently been restricted to problems of regional extent. The application of this approach at a global scale by Rodrigues *et al.* (2004) using data for several groups of terrestrial vertebrates thus represents an important development, supplementing the approaches identified in Table 1.

INTEGRATING PATTERN AND PROCESS

In an earlier section of this paper we discussed how varied the protected area system outcomes can be from taking different approaches to selecting areas, dependent for instance on the taxonomic level, and whether the emphasis is on richness, endemism, or perceived threats. This type of approach can be characterised as compositionalist, as such analyses provide an essentially static assessment of varying aspects of the present composition of the biota and seek to preserve the option value that comes from variety

(Williams & Araújo, 2000). We can contrast these approaches with more 'functionalist' approaches (Williams & Araújo, 2000, 2002), which focus on the potential viability of protected area networks projected into the future. Recently, attempts have been made within these grid-cell based 'complementarity' analyses to combine compositionalist and functionalist criteria based on assessments of the likelihood of persistence of populations in occupied grid cells into the future (e.g. Cowling *et al.*, 1999; Araújo *et al.*, 2002a; Williams & Araújo, 2002; Rouget *et al.*, 2003). In particular, accelerated climate change creates an urgent need to model species distributions and biogeographic patterns under multiple future scenarios (above).

Another interesting theme combining process with pattern emerges from recent work on the geography of range collapse as species head towards extinction. On the grounds that the centres of the range might be anticipated to provide optimal conditions for a species and the margins suboptimal habitat, it was thought likely that species would persist longest near their range centres (e.g. Brown, 1984; Curnutt *et al.*, 1996). This idea has led to the development of quantitative reserve-selection methods favouring conservation of species within the core of their current distributions (e.g. Araújo & Williams, 2000). Empirical evidence in support of this approach was offered in the form of observations that extinction probabilities of British-bird species in a particular 20-years' period were more likely in the edges of most species ranges than in the core (Araújo *et al.*, 2002a). This approach to reserve selection corrects the tendency of complementarity-based approaches to select 'ecotonal' areas in the intersection of many species ranges (Gaston *et al.*, 2001; Araújo & Williams, 2001). Paradoxically, some authors argue that reserves should indeed be located in areas of transition (Smith *et al.*, 2001; Spector, 2002) because this is where species' adaptation to future environmental changes is more likely. This discussion flags some of the most difficult debates in conservation biogeography: although it is true that species in transition zones are more likely to be subject to selective pressures that may favour genotypes with higher capacity to adapt in suboptimal conditions (e.g. produced by adverse climatic change conditions), it is also true that core populations are generally better adapted to cope with current environmental conditions. Ideally both core and peripheral populations should be conserved, but conservation resources are scarce and this degree of representation may not be achievable for more than a handful of species (Araújo, 2002).

To complicate the issue further, Channell & Lomolino (2000) have undertaken analyses of 309 declining species, using historical data, and have found that the predominant pattern is consistent with the 'contagion hypothesis' of range collapse, i.e. the extinction process first impacts a peripheral population, but then moves to drive more central populations to extinction, so that the last populations to persist are to be found (perhaps in isolates) towards a point on the historic range margin. Their analyses are based on recorded patterns of range change across continents and islands over long periods (centuries) and it remains to be shown if similar patterns and processes operate at fine scales of space and time (e.g. Rodríguez, 2002) or under conditions of particular directional shifts in climate. We are unsure how these

insights into the dynamics of range change should be fed into conservation planning (Channell & Lomolino, 2000; Araújo *et al.*, 2002b; Ceballos & Ehrlich, 2002; Rodríguez, 2002), but it is clearly an area worthy of more research efforts by conservation biogeographers. To come full circle with an earlier theme, it is well established in the biogeographical and palaeoecological literature that across much of the globe ecological systems have been continually resorted and reconstituted in response to pronounced climatic change over the Quaternary period. Species respond individualistically to these changes, and so species range locations, shapes and sizes have fluctuated through time. A combination of documentary and palaeoecological evidence provides the potential for improved insights into how species ranges change in size and configuration in response to both anthropogenic and natural forcing over a range of time frames.

CONCLUSIONS

Biogeographical traditions of thinking and analysis are important in many areas of conservation science, from coarse to fine scales of resolution of pattern, but are most evident and most significant working from the landscape, up to regional and thence to global scales of analysis. In the present paper, we have defined conservation biogeography in broad terms, but have necessarily illustrated the paper with only a limited set of topics, paying particular attention to strategic conservation planning. We think the latter focus is justified because of the contribution of biogeographical analyses in this important arena. We have also stressed that in this, as in other areas of conservation science, the approach taken in the analysis and interpretation necessarily involves the adoption of particular systems of social values, and that it is important to recognise this fact and to strive to provide guidance serving alternate valuations of nature and natural resources.

By selecting four principal themes by which to organise issues concerning the sensitivity of conservation biogeography to assumptions we hope to have highlighted important areas for future work, but have doubtless thereby neglected others. For instance, we have not explicitly discussed the many technical issues concerned with the proper analysis of spatially distributed data, and especially the concerns over spatial autocorrelation, and other artefacts such as the so-called geometric constraints problem (see, e.g. Diniz-Filho *et al.*, 2003; Hawkins & Porter, 2003; Colwell *et al.*, 2004; Dark, 2004).

To conclude this assessment, we may ask 'Where do we stand in conservation biogeography?' At one extreme we have authors who articulate the 'crisis' nature of the biodiversity conservation problem. They argue that we have all the data we need in order to make the key strategic decisions on mapping the biosphere and prioritising areas for protection at global and regional scales alike, we have to take decisions *now* to save as much as we can, and we have long established principles to guide reserve network design within regions, in terms of reserve sizes, connectivity, corridors, etc. Unsurprisingly, NGO-based proponents of global protected area planning frameworks take this sort of position, and emphasise the importance of developing '... a "grand synthesis"

of global priority-setting approaches so that we can speak with one voice to decision makers and donors about the fate of the biota on our planet' (Wikramanayake *et al.*, 2002, 242).

At the other end of this debate we may imagine the sceptic who contends that we do not yet know to within one, possibly two orders of magnitude what the present global species tally is, we lack systematic species range data of global extent (even for the best known taxa), that patterns of endemism are (in places) strongly correlated with patterns of collecting intensity, that theoretical guidelines for reserve systems are based on equivocal empirical data, and that there is huge uncertainty attached to our assumptions and models for protected area planning, and that in any event, no single conservation map can serve the diverse goals society may require. Moreover, such a sceptic may observe that international conservation NGOs have their own agendas, and need prioritisation schemes to 'sell' in the market place of biodiversity fund raising. These organisations have simultaneously engaged in developing the science, and advocating the outcomes, and have vested interests in defending the schemes they have developed and branded. Whilst we have highlighted many uncertainties and critical questions within the present article, we do not identify ourselves with such an extreme sceptical position: specifically we do not question the need for conservation action, we applaud the efforts of those in the NGO community who are so determined to do something about the problem, and we also welcome the emphasis on local and national leadership inherent, for example, in the recently floated multi-NGO Key Biodiversity Areas initiative.

We believe that the best defence against such sceptical views gaining hold (and they can readily be found in the wider discourse of the global internet) is for a broad section of the biogeography community to engage in independent development and evaluation of the scientific guidelines for conservation, spanning all aspects of conservation biogeography, and especially focussed on assessing the sensitivity of conservation guidelines to the assumptions inherent in our theories, models and analyses. We hope that this paper will make a small contribution towards developing this research programme. Such a programme offers enticing intellectual challenges and is of the greatest societal relevance. In short, we see conservation biogeography as having a central role to play in the conservation endeavour in the coming decades.

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