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Biogeography and macroecology: now a significant component of physical geography

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I Introduction

Since the previous review on biogeography and macroecology in this journal (Kent, 2005), the subject of macroecology appears to have gone from strength to strength. One key indicator of this vitality is the ISI Journal Citation Impact Factor for one of the key journals for the subject: *Global Ecology and Biogeography* – subtitled *A Journal of Macroecology*. The Impact Factor changed from a value of 1.02 in 2000 to 3.24 in 2004, 3.56 in 2005 and 3.31 in 2006. Even more remarkably in terms of physical geography, the same journal in 2005 had the highest ranking in the physical geography group (1/30) and was 16th in the much larger ecology group (16/112). In 2006, the journal was second in the physical geography group (2/30) and 21st in the ecology group (21/114; *Web of Knowledge*, September 2007). Clearly, macroecology is taking an increasingly significant place in the research agendas of both physical geography and ecology.

Underlying these trends is a burgeoning increase in the numbers of papers published that would qualify for inclusion in this review.

As a consequence, the review has to be necessarily selective, and papers are summarized below under a series of general headings.

II Macroecology as a subject

An excellent overview of macroecology is presented in the journal *Basic and Applied Ecology*, edited by Blackburn and Gaston (2004). The paper by Storch and Gaston (2004) that describes 12 statistical regularities in relation to large-scale species patterns that have been determined by macroecologists, and the listing of the factors behind these (energetic limitation, extinction probability, climatic variability, positive feedback in population dynamics and interspecific niche differences and habitat heterogeneity) is particularly valuable. Nevertheless, the debates and uncertainties over the exact nature of the subject, discussed in the previous review (Kent, 2005), still continue. The need to make all ecologists understand the macroecological agenda with the subjects of biology and ecology still dominated by reductionist approaches is a recurring theme (Blackburn, 2004).

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Ruggiero and Hawkins (2006) ignited a debate of particular interest to geographers when they argued that, although macroecology arose in part from geographical ecology (MacArthur, 1972), present trends in macroecology adopt a predominantly statistical approach to looking for rules and regularities that increasingly ignore the spatial distributional aspects linked to mapping that should make the subject essentially geographical in nature. In a vigorous reply, Blackburn and Gaston (2006) stressed that there is much more to macroecology than mapping, and emphasized that macroecological patterns will only be elucidated effectively through the formulation of relevant hypotheses and related statistical approaches. As most geographers know, maps are only one of many tools in the geographers' armoury and the debate is in many ways fascinatingly reminiscent of those that pervaded geography during the so-called 'Quantitative Revolution' of the 1960s and 70s.

Other ongoing discussion at the core of the subject concerns neutral theory in ecology and its relevance to hypothesis generation in macroecology (Blackburn and Gaston, 2004; Maurer and McGill, 2004; Gaston and Chown, 2005; Hu and He, 2006). Neutral models assume that all individuals at particular trophic levels in ecosystems are ecologically equivalent. Community patterns that emerge under this assumption can then be compared with those in real world communities.

Further discussion centres on scale in macroecology and the links between bottom-up and top-down approaches and how the importance of variables and factors changes as one moves up or down in spatial scale (Gripengberg and Roslin, 2007). Rahbek (2005) has reviewed the literature on distributions of species richness in relation to altitudinal gradients and shows how scale effects ('extent' and 'grain size') affect the elucidation of underlying patterns and processes. She presents a six-point agenda for analysis of species

richness/environment gradient relationships, taking scale effects into account. Pautasso (2007) showed how the widely observed correlation between human population density and vertebrate and plant species richness is scale-dependent in terms of both extent and grain size and the correlation turns from positive to negative below a study grain of c. 1 km and below a study extent of c. 10 000 km². Again, Burns (2004) demonstrated how macroecological patterns in seed dispersal mutualisms are scale-dependent in both space and time, with mutualistic relationships between fruits and frugivores emerging as important at some scales, while at other scales, climatic, phylogenetic and historical factors are more significant.

Macroecological patterns and relationships for critical plant traits are gradually emerging. A recent significant advance is the examination of global patterns in seed size (Moles *et al.*, 2007). A 320-fold decrease in geometric mean seed mass was found between the equator and 60°. However, this decline is not linear and, on the border of the tropics, a very rapid sevenfold fall in mean seed mass was detected, which appeared to be most closely correlated with changes in plant growth form and vegetation type, indicating a possible sudden change in plant strategy at the edge of the tropics.

On a broader front, Lomolino *et al.* (2006) have called for the search for ecogeographical rules (Bergmann's rule; Rapoport's rule; Brown's rule; Foster's 'Island rule') in macroecology to adopt a more integrated research agenda, with studies that simultaneously examine varying clines in species morphology, geographical ranges and diversity and their interrelationships. Rather than just describing patterns, macroecological research should devise and then test causal hypotheses that aim to explain patterns, and they list 10 key points for this more integrative research agenda.

Lastly, in a key paper, Blackburn *et al.* (2006) reviewed 279 abundance-species

range distribution relationships, finding a strong positive association between the variables. However, the strength of relationships varied across realms, with the strongest in the marine and intertidal group, intermediate relationships in terrestrial and parasitic assemblages and the weakest in fresh water. Also, Chown *et al.* (2004) have made the case for macrophysiology – the study of variability in physiological traits over large spatial and temporal scales and the underlying ecological factors behind this variability. They argue that, first, despite substantial human impact, the relationships between animal diversity and ecosystem function are not well understood and, second, that limited macroecological research has indicated possible major differences in the physiological structure and functioning of Northern and Southern Hemisphere systems.

III Methods in macroecology

In three excellent overviews of methodological approaches to macroecology, Blackburn (2004), Fortin *et al.* (2005) and Rahbek (2005) have stressed the need for the development of new statistical approaches that take account of the problems of spatial dependency and spatial and phylogenetic autocorrelation that are present in most macroecological data. Similar comments on spatial autocorrelation and dependency in macroecological data are made by Carl and Kühn (2007), Dormann (2007) and Osborne *et al.* (2007), who examined the application of geographically weighted regression (GWR) and varying coefficient modelling (VCM) in predictive mapping of bird populations in Spain and Britain in order to overcome these problems. Likewise, Bahn *et al.* (2006) modelled bird populations in the United States using 10 years of US Breeding Bird Survey data and spatially explicit autocorrelation models that accounted for spatial autocorrelation and enabled partialling out of the spatial component of the bird distributions. Again, McPherson and Jetz (2007)

constructed four maps of bird species richness (range maps; field-derived bird atlas data; logistic and autologistic distribution models) across 13 nations in southern and eastern Africa and erected five explanatory hypotheses for the distributions. Due to the varying nature of the underlying data types, variations in the underlying spatial autocorrelation structure affected which hypothesis appeared to best describe each of the four mapped patterns.

An alternative approach to accounting for spatial autocorrelation, eigenvector-based spatial filtering, was presented by Diniz-Filho and Bini (2005), when examining South American bird distributions in relation to climatic and energy (annual actual evapotranspiration – AET) variables. Geographical coordinates of the grid data were analysed using the Principal Coordinates of Neighbour Matrices (PCNM) program of Borcard and Legendre (2002) and Borcard *et al.* (2004) to perform eigenanalysis of geographical distances to derive a set of spatial filters (eigenvectors) that represent the spatial structure of the region at different spatial scales (Griffith, 2003). Kühn (2007) showed how, allowing for spatial autocorrelation when looking at relationships between species richness and altitude in plant species in Germany, the correlation/regression relationship changed from positive, when there was no account taken for spatial autocorrelation, to negative, when it was. This was explained by the north–south altitudinal gradient inverting the larger-scale patterns of equator to pole. Carl and Kühn (2007) also illustrated the wider potential applications of Gaussian and logit models, using simulated data and plant species richness data from Germany.

Perhaps most importantly of all, Rangel *et al.* (2006) introduced their SAM (Spatial Analysis in Macroecology) computer software package, which gathers together a set of statistical tools for describing spatial structures and hypothesis testing into an explicit spatial

framework for techniques of regression and correlation. In particular, Moran's I statistic as a measure of spatial autocorrelation is made available with significance testing, as well as a Local Indicator of Spatial Autocorrelation Analysis (LISA). In terms of spatial filtering, Trend Surface Analysis (TSA) is included, together with the Principal Coordinates of Neighbour Matrices (PCNM) program of Borcard and Legendre (2002) and Borcard *et al.* (2004) mentioned above. A wide range of regression methods that allow for spatial autocorrelation is offered. The package is available as freeware and has a user-friendly graphical interface.

Various authors have explored the effectiveness of differing methods for modelling species distributions as well as the properties of different data sets, and Araújo and Guisan (2006) present five challenges for species distribution modelling: (1) clarification of the niche concept; (2) improved designs for sampling data for building models; (3) improved parameterization; (4) improved model selection and predictor contribution; and (5) improved model evaluation. Segurado and Araújo (2004) compared seven modelling techniques (Gower metric; Ecological Niche Factor Analysis; classification trees; neural networks; generalized linear models; generalized additive models; and spatial interpolators) on distributions of 44 herpetofaunal species in Portugal. No one technique was suitable in all circumstances and they concluded that an appropriate method depended on the properties of the distribution being studied, the scale and the goals of the modelling. Using artificial data for 18 species generated over a real landscape (California), Meynard and Quinn (2007) compared four sets of models: general additive models (GAM), with and without flexible degrees of freedom; logistic regressions (general linear models GLM), with and without variable selection; classification trees and the genetic algorithm for rule-set production (GARP). GAM outperformed all other methods, with

GLM close behind, and an expert-based variable selection method was considered preferable to those based on automated procedures.

Tsoar *et al.* (2007) compared six distribution modelling methods using only presence-absence data and found comparatively small differences between models, although the distributional properties of the species (narrow as opposed to broad species ranges) were shown to have effects on predictive accuracy. The effect of species range sizes on the accuracy of distribution models was also examined by McPherson *et al.* (2004) using 32 endemic bird species in South Africa, Lesotho and Swaziland. They concluded that most reported effects of range size or rarity on model accuracy appeared to be artifacts linked to particular methods, rather than representing ecologically meaningful effects. The reliability of models needs to be judged with great care.

Publications relating to other issues in macro-ecological methods include: the potential value of long-term monitoring (LTM) data as a basis for analysis (Brotons *et al.*, 2007); annexes to papers and books on avian diets as sources of data for macroecologists (Grim, 2006); the limitations of ecological journal papers in providing suitable data for macroecological analyses and the need for underlying data from journal papers to be stored in electronic archives that are then open to researchers looking for large-scale data sets (Pärtel, 2006); the robustness of the secondary data sources that are widely used in macroecology (Mathias *et al.*, 2004); effects of variations in grid cell size on determination of species richness/climate relationships (Nogués-Bravo and Araújo, 2006); the effects of plot area on estimation of avian abundances (Pautasso and Gaston, 2006); and the problems in methods for both mapping and for determining the boundaries of species ranges and mapping species richness (Fortin *et al.*, 2005; Graham and Hijmans, 2006).

IV Species range size distributions and range size variations

Initial studies of global macroecological patterns have been completed in birds by (Orme *et al.*, 2006), raptors and owls (Gaston *et al.*, 2005) and parrots (Blackburn *et al.*, 2004). In birds, range size does not follow a straightforward latitudinal pattern and smallest range sizes occur on islands, mountains and in the Southern Hemisphere. The global species range size distributions for raptors and owls are severely right-skewed on untransformed axes and are not lognormally distributed as is often the case. In parrots, Blackburn *et al.* (2004) looked at nine measures of range size using differing spatial resolutions and found little variation between them.

In plants, Pohlman *et al.* (2005) examined range size, seedling ecophysiology and phenotypic plasticity in *Acacia* species in Australia, while Lowry and Lester (2006) studied the relationship of range size to mating system and genomic structure in *Clarkia* in western North America. Using data from four species of Proteaceae in South Africa, Pearson *et al.* (2006) investigated the effects of nine different modelling methods for potential changes in species range sizes in relation to present and future climates and showed predictions to vary significantly in direction and magnitude, thus indicating a considerable degree of uncertainty in predictive models of species range sizes. Schurr *et al.* (2007), again looking at the Proteaceae in South Africa, evaluated the way in which plant species fill their potential range by means of colonization and persistence ability. Further indications of the effects of dispersal ability on species range size are provided for marine taxa by Lester *et al.* (2007), with somewhat equivocal results. For other organism groups, Harcourt (2006) has looked at range size in primates, while Rundle *et al.* (2007) found that range size in North American *Enallagma* damselflies is correlated with wing size. Lastly, using neutral modelling techniques, Mouillot and Gaston (2007) showed that statistically significant heritability (the property

that species that are closely related phylogenetically tend to have similar sized species ranges) can be found.

V Species range size/richness relationships and the 'mid-domain effect'

The past few years have seen a major debate on the subject of the 'mid-domain effect' (MDE). The MDE is a null model, originally derived by Colwell and Hurtt (1994) and refined by Willig and Lyons (1998) and Colwell and Lees (2000), that predicts, for a given bounded (geometrically constrained) domain or area, how species richness will be distributed in space in the absence of environmental gradients. It predicts a pattern, produced by the random overlap of species geographic ranges, that is characterized by the highest species richness in the centre of the domain, with lower richness at the margins – hence 'the mid-domain effect'. Colwell *et al.* (2004) reviewed the whole idea, which has been subject to criticisms by Hawkins and Diniz-Filho (2002), Laurie and Silander (2002) and Zapata *et al.* (2003). A themed section of the journal *The American Naturalist* presented opposing viewpoints (Colwell *et al.*, 2005; Zapata *et al.*, 2005), with an overall evaluation by Hawkins *et al.* (2005). A major problem appears to be that the range size frequency distribution under uniform environments without environmental gradients does not exist, so that the MDE cannot in practice be considered a proper null model that species response to environmental gradients can be tested against. The debate continues with further contributions by Rangel and Diniz-Filho (2005), Storch *et al.* (2006), Dunn *et al.* (2007) and McClain *et al.* (2007), and an empirical study of the MDE on moth species richness along a tropical elevation gradient (Brehm *et al.*, 2007). Kerr *et al.* (2006), Currie and Kerr (2007a; 2007b) and Lees and Colwell (2007) present ongoing arguments over testing of the MDE on birds and mammals in Madagascar.

Species range size/abundance, as opposed to richness, relationships have also been

examined with contributions by Sagarin and Gaines (2006) on the assumption that species are most abundant in the centre of their range (Brown's principle), Gilman (2005) on the same assumption in an intertidal limpet on the Pacific coast of North America, and Symonds and Johnson (2006) on Australian passerines.

VI Body size/range size relationships, body size latitudinal gradients and body size/abundance relationships

Diniz-Filho *et al.* (2005a; 2005b) examined body size/range size relationships in New World carnivores using the constraint envelope approach and found links between geographical range size, minimum viable geographical range size and extinction risk. Murray and Hose (2005) showed that body size/range size relationships in Australian frogs disappeared after accounting for species abundance and egg size. Bergmann's rule, that body size tends to be linearly correlated with latitude, continues to be tested, with Jones *et al.* (2005) demonstrating evidence in a Neotropical songbird (*Dendroica cerulea*). Working with European mammals, Rodriguez *et al.* (2006) showed that, although many endothermic species do follow the rule, some do not. They conclude, first, that the relationship is probably non-linear for large-scale studies, rather than linear; second, that the dependence of endothermic species is probably dependent on more than just temperature; and, third, that human impacts, particularly via extinctions, confuse the picture. European and North American anurans (frogs and toads) were shown to follow Bergmann's rule, while urodeles (salamanders) do not, by Olalla-Tárraga and Rodriguez (2007), a result linked to the heat balance hypothesis.

Body size/abundance relationships have been reviewed by White *et al.* (2007), who suggest that confusion has occurred between four different, but interrelated, relationships – the global size/density relationship, local size/density relationships, individual size

distributions or size spectra, and cross-community scaling relationships. They seek to clarify these to improve the formulation of research goals in this area of macroecology.

VII Latitudinal species range and richness (diversity) relationships

Rapoport's rule (that geographic range size of species increases from equator to poles) continues to attract much attention in research (Rapoport, 1982). Ribas and Schoereder (2006) tested the Rapoport effect using null models and simulated data against real data from the literature. Results were inconclusive with some significant patterns emerging but no overall consistent global relationships, a similar result to that of Weizer *et al.* (2007), working with New World woody plants. In contrast, Ruggiero and Werenkraut (2007) found that the Rapoport effect appeared to be strong on the continental land masses of the Northern Hemisphere on the basis of a meta-analysis of 49 published studies. Likewise, Arita *et al.* (2005) confirmed the validity of Rapoport's rule for the mammals of North America and similar results were found by Morin and Chuine (2006) and Lane (2007) for northern temperate/boreal trees. More mixed results were demonstrated by Stevens (2004), researching New World bat communities. Confirmation of the rule for marine molluscs on both the Pacific and Atlantic seabords of both North and South America was obtained by Fortes and Absalão (2004), while more complex global patterns of species richness in marine molluscs were revealed by Rex *et al.* (2005).

A special feature in the journal *Ecology* (Hawkins and Agrawal, 2005) looked at latitudinal gradients in species richness. Field *et al.* (2005) present new global models for predicting woody plant species richness in relation to water and energy availability. Stohlgren *et al.* (2005) examined the diversity of invasive plant species along latitudinal gradients in the United States, with their methods and conclusions, particularly, that

the best predictor of density of non-native species was the density of native species, being challenged by Fridley *et al.* (2006).

Orme *et al.* (2006) looked at bird species range sizes at the global scale and found that the pattern for latitudinal size range was complex with latitudinal range size actually decreasing from low to high latitudes – the opposite of Rapoport's rule. There was no decrease in geographic range size towards the tropics, but the largest ranges were in high northern latitudes. The importance of taking a global view was emphasized. Lastly, Hernández Fernández and Vrba (2005) examined the Rapoport effect in African mammals in relation to climatic variability and found that, although latitudinal species range relationships occur, there are differing explanations between the Northern and Southern Hemispheres, linked to the presence of land connections with Eurasia to the north.

VIII Species/energy relationships

One of the most widely recognized macroecological patterns is the positive relationship between the species richness and available energy across the surface of the earth (Bonn *et al.*, 2004; Clarke and Gaston, 2006; Mittelbach *et al.*, 2007). Various competing hypotheses have been put forward to explain this relationship (Cardillo *et al.*, 2005; Evans *et al.*, 2005a; 2006a; Mittelbach *et al.*, 2007). Evans and Gaston (2005a) reviewed the evolutionary-rates hypothesis (high environmental energy promotes faster molecular activity, that in turn encourages higher rates of speciation) with equivocal results, while Hawkins *et al.* (2007a; 2007b) assessed the climatically based energy hypothesis, which uses measures based on energy, water or energy/water balance (Hawkins *et al.*, 2003). Bini *et al.* (2004) found support for climatically based hypotheses working on bird orders in South America. Whittaker *et al.* (2007) reviewed Hawkins's water/energy conjecture using species from five

different taxa in Europe and found general support for the hypothesis and the idea that water is more limiting in southern Europe, while energy is more limiting in the north. However, both papers conclude that many problems remain in relation to modelling, linked to complicating altitudinal gradients and human impact factors.

A key point is that available energy is often equated with temperature but temperature is not the same as energy. Photosynthetically active energy (PAR) is a better measure, expressed in terms of net primary production, but there is also Gibb's free energy that is retained in the reduced carbon compounds that constitute tissue (chemical energy) (Clarke and Gaston, 2006).

Swenson and Waring (2006) modelled woody plant species richness across the northwestern United States at three scales and found modelled gross photosynthesis to be a good predictor of richness in both trees and shrubs. Using data on British birds, Evans *et al.* (2005a) explored species/energy relationships using different measures of environmental energy availability, and Evans *et al.* (2006b) examined individual species/energy relationships in relation to bird species traits such as niche breadth. Storch *et al.* (2005) looked at the three-dimensional species/area/energy relationships in relation to South African bird data, finding that the slope of the species/area relationship is lower in areas with high availability of energy, while the slope of the species/energy relationship is lower for larger areas.

Evans and Gaston (2005b) and Evans *et al.* (2005b) investigated the positive correlations between species richness, energy availability and human population density. On the one hand, the results imply that high human population densities reduce the rate at which species richness increases with energy availability. On the other, high energy availability with high human population density exerts a positive effect on exotic species richness.

IX A metabolic theory of ecology

The debate on the basis and nature of a metabolic theory of ecology continues but there is insufficient space to be able to present full details here. Brown *et al.* (2003; 2004a) have clearly laid out the underlying principles and concepts. Metabolic rate is the rate at which organisms take up, transform and expend energy and materials and the theory predicts how metabolic rate varies with body size, temperature and stoichiometry (the quantities, or proportions of chemical elements in different entities, for example, organisms or their environments). Ecological processes at all levels from individual organisms to the biosphere are controlled by metabolic rate, which sets the rate at which resources are taken up from the environment and are allocated to growth, survival and reproduction. Resources are distributed within branching networks and the fractal nature of these networks results in the finding that supply rates and thus the metabolic rates scale as a $\frac{3}{4}$ power of body volume – the allometric exponent (West *et al.*, 1997; West, 1999). A themed section of the journal *Ecology* presented a range of viewpoints on the attractiveness and validity of the theory, including papers by Harte (2004), Marquet *et al.* (2004), Tilman *et al.* (2004), Cyr and Walker (2004), Cottingham and Zens (2004) and Horn (2004), with a final reply by Brown *et al.* (2004b).

Much further debate has ensued, notably in a series of Forum-themed sections of *Functional Ecology* between 2004 and 2006 centred on the final links of the fractal branching network, the validity of the $\frac{3}{4}$ power law and the relationships between temperature and metabolic rate (Clarke and Fraser, 2004; Clarke, 2004; 2006; Kozłowski and Konarzewski, 2004; 2005; Savage *et al.*, 2004; Brown *et al.*, 2005; Etienne *et al.*, 2006; Gillooly *et al.*, 2006), plus articles by van der Meer (2006), O'Connor *et al.* (2007) and Allen and Gillooly (2007) that are primarily concerned with the mechanistic basis of the theory. Ecological stoichiometry

(the study of the balance of chemical elements within ecological processes) has also been the focus of a set of related papers in the journal *Oikos*. Moe *et al.* (2005) examine the implications of ecological stoichiometry for community and population ecology, Schade *et al.* (2005) provide a conceptual framework for ecological stoichiometry linking biogeochemical patterns at global level to the physiological limitations that operate at the level of the individual organism or cell and Ptacnik *et al.* (2005) discuss the implications of ecological stoichiometry for the sustainable acquisition of ecosystem services and the varying scale of impacts of carbon, nitrogen and phosphorus when presented to organisms in differing ratios in space and time.

Recently, the first tests of some of the theoretical predictions of metabolic theory have emerged. Hawkins *et al.* (2007a) tested the prediction that log-normal transformed species richness gradients are linearly associated with a linear, inverse transformation of annual temperature, with a slope of around -0.65 . Using a set of 46 data sets from a wide range of terrestrial plant, invertebrate and ectothermic vertebrate groups from all over the world, they used ordinary least squares (OLS) and reduced major axis (RMA) regression to test this proposition. Of the 46 data sets, only one was consistent in meeting the above prediction using OLS and none were consistent using RMA. Weak results were also found for the predicted slope of the line using both methods. They concluded that metabolic theory is a poor predictor of species richness gradients and that the relationship between species richness and temperature is also affected by taxonomic and geographical variability, aspects that are discussed further by Latimer (2007). Gillooly and Allen (2007) give a spirited reply to these findings, while Hawkins *et al.* (2007b) respond with equal vigour. Others have also begun to test the predictions of the theory. Algar *et al.* (2007) sought to test the species richness gradient-temperature relationship,

using a range of data sets for different species groups in North America. They found most relationships to be curvilinear, thus failing to support the predictions of the theory. However, Hawkins *et al.* (2007a) point out problems with their predicted slope value of -0.78 , rather than -0.65 , caused by a rescaling of annual temperature values in Allen *et al.*'s paper of 2002 and by the fact that they only used OLS regression, whereas the original theory used RMA, giving different predicted slope values for the regression line. Mueller-Landau *et al.* (2006) tested the prediction of metabolic theory that tree abundances will scale at the -2 power of diameter and certain predictions of demographic equilibrium theory (DET). Using 14 large-scale tropical forest plots, they found that the data were uniformly inconsistent with the predictions of metabolic theory but much closer to the predictions of DET, particularly relating to the significance of local site conditions that lead to differences in tree growth and mortality. Finally, Russo *et al.* (2007) reported that they were unable to demonstrate that the exponent of the growth/diameter scaling relationship in a wide range of New Zealand forests was $1/3$, nor that small and large individuals are invariant in their exponent, or that tree height scales with diameter.

X Macroecology, human impact and biological conservation

Gaston (2005; 2006) and Webb *et al.* (2007) have emphasized the importance of accounting for human impact when analysing and interpreting macroecological patterns, particularly the relationships between human population density and species richness, abundance and ecosystem productivity (net primary production). Davies *et al.* (2006), using a global database for birds, showed that, after controlling for species richness, measures of human impact are the best predictors of extinction risk. Evans *et al.* (2006b) demonstrated positive species-human relations in anuran and avian species in South Africa and Evans *et al.* (2007) showed the

same relationships for avian species richness in Britain and the fact that they are not attributable to sampling bias in ornithological recording. Working in Australia, Luck (2007) confirmed the relationship between human population density, species richness of birds, butterflies and mammals, and net primary production, and made suggestions for the stabilization or reduction of population in areas of high productivity and species richness to facilitate conservation. Araújo and Rahbek (2007) responded with comments on the problems of taking species richness as a primary criterion for selection of protected areas and stressed the value of complementarity (the choosing of areas for protection that differ from each other in species composition to maximize conservation of the overall range of species in a region).

The description, analysis and prediction of changes in species ranges due to human impact through habitat destruction and climate change is increasingly important. La Sorte (2006), working on species ranges in birds in North America between 1968 and 2003, revealed that more species (51%) exhibited patterns of range expansion than contraction (28%) and showed the substantial role of human impact in these changes. Rodriguez *et al.* (2007) reviewed the application of predictive modelling of species distributions to biodiversity conservation and presented a collection of related methodological papers (see section III above). Bini *et al.* (2006) developed models to predict the range size and location of hypothetical non-described species to try to overcome the so-called Linnean (many species on earth are still not formally described) and Wallacean (the distributions of most taxa are not fully known and there are many gaps) shortfalls. The resulting models suggested that inclusion of many new hypothetical species ranges would require extensive revisions to existing networks of protected areas. Lastly, Gaston and Fuller (2007) have stressed the message from macroecological studies on the importance of conserving species which

are common and widespread but which can still undergo catastrophic collapse and extinction, due to human impact. In the past, the emphasis in preventing extinctions has always tended to be on species that have small populations and limited ranges.

XI Conclusions

As both the statistics presented at the outset and the range of this review demonstrate, research in macroecology is now a very significant and important part of biogeography and physical geography. However, the geographical community has been extremely slow to realize this, and the vast majority of research to date has been completed by biologists with an interest in large-scale spatial patterns and their underlying processes rather than by geographers themselves. If biogeography is to maintain its role within physical geography, a much more serious consideration of the role and relevance of macroecology to the discipline is required.

Macroecology itself has rapidly developed into a fascinating subject but, as many elements of this review illustrate, the complexities of macroecological patterns, their underlying processes and the confounding effects of human impact all combine to make the search for clear and unambiguous relationships between species distributions, abundance and causal factors at regional, continental and global scales a difficult and demanding task.

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