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# Biogeography and macroecology

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## 1 The evolution of macroecology

One of the most interesting and important areas of growth within the disciplines of biology and ecology over the past 10–15 years has been the subject of macroecology. The origins of the subject are attributed to Brown and Maurer (1989) and to the textbook entitled *Macroecology* published by James H. Brown in 1995. Macroecology has been defined as ‘the study and understanding of the division of food and space among species at large spatial (geographical) and temporal scales’ (Blackburn and Gaston, 2003a: 6). Large spatial scales correspond to national, regional, continental and global levels. Somewhat confusingly, these have been referred to as ‘geographic scales’ by researchers in the field. Large scale, however, is taken as corresponding to species and environmental variation over large areas and small scale to variation over small areas (Gaston, 2003).

### 1 Macroecology and biogeography

Macroecology has been seen by some as being very similar to biogeography, which seeks to describe and explain patterns of species distributions often, but not always, at large spatial scales. However, proponents of macroecology describe it as a distinctive approach to research in ecology that is distinct from biogeography, which not only examines patterns of species distributions but

also seeks to discover natural laws and unifying principles which underpin the nature, structure and function of ecological systems. Thus macroecology overlaps with biogeography but the goals of macroecology extend beyond mere description and explanation of species’ spatial patterns to the uncovering of fundamental relationships between species ranges, abundance, diversity, body size and environmental correlates, such as temperature and ecosystem energetics at these large spatial and temporal scales. It thus overlaps the fields of biogeography, ecology, palaeoecology/palaeobiology, (macro)evolution and even palaeontology. An interesting debate in the journal *Nature* in 2002 centred on the above points and the differences between biogeography and macroecology (Nee, 2002; Blackburn and Gaston, 2002a; Fisher, 2002; Marquet, 2002). From the physical geography perspective, however, with only a few exceptions (e.g., Whittaker *et al.*, 2001; 2003; Willis and Whittaker, 2002), the majority of developments in macroecology have come from researchers based in university departments of biology and ecology, rather than from staff within departments of geography and thus physical geographers.

### 2 Macroecology comes of age

Macroecology can be said to have come of age in 2003, with the publication of two

important texts on the subject. First, Blackburn and Gaston (2003b) edited the proceedings of the 43rd Annual Symposium of the British Ecological Society on the subject, held in April 2002, which contain contributions from virtually all the leading researchers. Secondly, Kevin Gaston published his book entitled *The structure and dynamics of geographic ranges* (Gaston, 2003), which represents a key text for all biogeographers. Also, since 1999, the sister journal of *Journal of Biogeography*, namely *Global Ecology and Biogeography*, has adopted the subtitle of *A Journal of Macroecology*, a point that is not lost on either Blackburn or Gaston, who hint that they might prefer the main title of the journal to be *Journal of Macroecology* (Blackburn and Gaston, 2002b).

Macroecology as a branch of ecology is not entirely new, however. As pointed out by Brown *et al.* (2003a), it has its roots in the work of Arrhenius (1921), Willis (1922), Preston (1948; 1960; 1962), MacArthur (1957; 1960; 1965; 1972), MacArthur and Wilson (1963; 1967) and Whittaker (1967).

### 3 Areography

The book by Gaston (2003) is primarily centred on areography. Areography is a component of macroecology that is probably much closer to the more restricted definition of biogeography above, in that it is concerned with species' geographic ranges (i.e., their distributions) and the properties of those ranges, such as their edges and boundaries, range size and shape, range overlaps between species and the relationships of all of these with species abundances (Brown and Lomolino, 1998). The notion of areography comes from the publication of the English-language version of a text with that name by an Argentinian ecologist, Eduardo Rapoport, in 1982.

### 4 Criticisms of the macroecological approach

Macroecology and areography have had a somewhat hesitant birth over the past decade that is reflected in a number of articles in the

literature (Blackburn and Gaston, 1998; 2002b; Gaston and Blackburn, 1999; Lawton, 1999; Gaston, 2000). A range of criticisms has been levelled at the whole approach and these have been rebutted in an extremely spirited manner by the above authors. As Brown (1995; 1999), Gaston and Blackburn (1999) and Maurer (1999) cogently argue, ecologists have adopted a predominantly reductionist approach over the past 30 years, and a prevailing view is that it is only through synthesis from such microscopic ecology that the larger picture may be seen – the 'bottom-up' approach. Brown and others argue, however, that the 'top-down' rather than the 'bottom-up' approach has much to recommend it and indeed that there are many large-scale patterns and processes that are never going to be elucidated from synthesis from even a wide range of reductionist research alone. This is not to dismiss that approach. Both have their value, but the large-scale approach has been comparatively neglected.

A series of issues arises, however, with respect to research design in macroecology.

1. For the past 20 years or so, experimental ecology using deductive scientific method has dominated ecology and biology. This means that carefully controlled manipulative experiments with suitable statistical designs and replication are employed (Blackburn and Gaston, 1998; 2003a; Gaston and Blackburn, 1999). In contrast, a great deal of macroecological work employs a more inductive and descriptive/observational approach, often based on multiple working hypotheses (Chamberlin, 1965; Gaston and Blackburn, 1999). The major difficulty with such observational data is that, although they may be able to indicate relationships between macroecological variables, they are often poor at separating out alternatives in terms of explanation. Framing of clear null hypotheses using observational data is essential (Gaston and Blackburn, 1999; Blackburn and Gaston, 2003a), since

failure to do so may often allow acceptance of a macroecological pattern as having a biological/ecological explanation, when in reality it may be an artifact of the particular methodology or data employed (Brown, 1999).

Although possibilities for manipulative experiments are clearly limited, Gaston and Blackburn (1999) and Blackburn and Gaston (2003a) emphasize the potential importance of 'natural experiments' at the large spatial and temporal scales of macroecology. Examples of these are major natural disasters, such as fires, earthquakes, floods and volcanic eruptions or longer-term temporal changes due to climate change or ever-increasing anthropogenic impact on ecosystems and species assemblages. A perhaps paradoxical aspect of these is that they represent uncontrolled experiments but in this respect are much closer to the 'real world' situation than most manipulative highly controlled experiments within reductionist ecology.

2. The quality of data used in macroecology is critical, but inevitably most data are taken from secondary sources – biological atlases and databases, international and national censuses, syntheses of published papers or archive records, which will have often been collected by multiple recorders and where the quality and consistency of the data may be highly variable (Mathias *et al.*, 2004). Large-scale environmental data are also often available but many of the same problems apply. Spatial resolutions of different databases and atlases will also often vary (Blackburn and Gaston, 1998; Gaston, 2003; Blackburn *et al.*, 2004). Data on bird and insect species tend to be used preferentially in analyses, partly because of their obvious mobility and sensitivity to spatial and temporal change, but also because databases are probably most widely developed in these areas. Nevertheless, Gaston and Blackburn (1999), Blackburn *et al.* (2004) and Mathias *et al.* (2004) argue that, despite these potential

problems of data quality, broad-scale patterns will often be relatively unaffected, although potentially important effects on more detailed variation are more likely. Further research is required into all these aspects of data quality.

3. As Gaston and Blackburn (1999; 2000) and Maurer (1999) stress, methodology and techniques, particularly those for statistical analysis, are not yet sufficiently developed. Blackburn and Gaston (1998) describe the problems of the absence of controls in much macroecological research and the care that is necessary in the formulation of hypotheses. They also highlight the problems of the skewed distributions often found in species data and whether or not they should be normalized, the importance of including understanding of phylogeny and its implications for the species as the basic unit of analysis (also highlighted in Freckleton *et al.*, 2003) and finally the difficulties of interpretation of the commonly observed polygonal or space-filling and also the frequent nonlinear bivariate scattergrams that often result from comparison of macroecological variables.

Macroecological patterns are often complex and are thus not amenable to the application of conventional statistical analysis. Data are usually spatially or temporally referenced and may thus frequently exhibit spatial and/or temporal autocorrelation that will need to be accounted for (Carroll and Pearson, 2000; Lennon, 2000; Lennon *et al.*, 2001; Diniz-Filho *et al.*, 2003; Kent *et al.*, 2005). New approaches to spatial and temporal data analysis are being developed but significant problems remain, notably the overreliance on linear statistical models and the need to take account of spatial and temporal autocorrelation in multivariate analysis.

4. Scale in macroecology – Blackburn and Gaston (2002b) argue that there is no one 'best' scale for ecological research and that overemphasis on either small-scale research in reductionist ecology or on patterns and

processes at the largest scale is dangerous. More importantly still, Whittaker *et al.* (2001) and Willis and Whittaker (2002) have stressed that the factors determining the diversity and distribution of organisms will vary at different spatial and temporal scales. They believe that a hierarchical approach is necessary, where processes are nested according to both spatial and temporal scales. Some similarities will exist in the roles of controlling factors between varying scales, but, more often than not, different variables will emerge as being important at different scales and thus relationships between macroecological variables will also vary.

Links between species diversity, trophic structure and spatial scaling theory have also recently been explored by Brose *et al.* (2004). Burns (2004) has also shown how studies on macroecological patterns in seed dispersal mutualisms are scale-dependent in both space and time.

## II Recent developments in key areas of macroecology

### 1 Species range size distributions and range size variation

Gaston (2003) is the major work of synthesis in this area and focuses on the themes of range edges and the factors limiting species distributions; patterns in species range size variation and the variance in species abundance structures over their ranges. Species range size distributions tend to be markedly right or positively skewed – most species have limited distributions and comparatively few are widespread. Gaston and He (2002) present a new model for this distribution of range sizes using a stochastic differential equation, which is then tested successfully against empirical range size distributions.

Webb and Gaston (2003) found that range size is not ‘heritable’ – i.e., variation in range size is explained more by geographical/environmental factors and ‘the history of place’

than by intrinsic biological traits. However, this view is challenged by Diniz-Filho (2004), who argues that variation in body size, as a highly ‘heritable’ trait at the species level, can be partitioned into anagenetic and cladogenetic components. Furthermore, anagenetic trends behind Bergmann’s rule, that endothermic species in cooler climates, which are mostly at higher latitudes, are generally larger than their relatives in warmer areas (Bergmann, 1847), are counterbalanced by the available habitat area or continental edges limiting overall species distribution at higher latitudes, which increases the extinction probability. Extinction will also occur at smaller body sizes for species subject to these constraints at high latitudes and the body size distribution for the entire fauna will become more right-skewed.

### 2 Species occupancy-abundance models

Many studies have clearly shown the general positive relationship between species occupancy and abundance – species that are locally abundant are often widely distributed in space, while rarer species tend to have limited spatial extent (Gaston *et al.*, 2000). Gaston and Blackburn (2000) and Gaston (2003) review the literature and the mechanisms that may explain this relationship. He *et al.* (2002) evaluated existing mathematical models of the relationship, developing a unified three-parameter model, within which six variants were examined. Gaston and Blackburn (2003a) tested the prediction that deviations of British bird species from the positive interspecific relationship between abundance and occupancy were caused by differences in dispersal. Results were essentially negative, with the only consistent predictor of occupancy being population size.

Moving away from the primary focus on avian and insect faunas, in marine ecology, Foggo *et al.* (2003) tested abundance–occupancy relationships for British estuarine macroinvertebrates, while Frost *et al.* (2004) similarly investigated them for British sandy beach macrofauna. In both cases, significant positive relationships were found with

comparatively little variation among taxonomic groups but, as in most other studies, substantial unexplained variation remained. Precise understanding of the mechanisms behind the relationships remains elusive.

### 3 Body size-range size relationships and body size-latitude gradients

Another commonly stated relationship in macroecology is that small-sized species tend to have smaller geographical ranges than large-sized species (Gaston, 2003). However, the relationship more often tends to be of triangular form, i.e., at large geographic ranges species of all sizes may occur, with the upper limit determined by the size of the study area, while at smaller ranges there is more evidence of a positive relationship between range size and body size. One explanation for this is that larger-bodied species with small geographical ranges will have a higher probability of extinction (Diniz-Filho, 2004). Biedermann (2003) examined body size-area relationships across habitat patches of increasing size in 15 different landscapes ranging from central European grassland to Asian tropical forest, and found that incidence increased with body size and thus body size is a rough predictor for the area requirements of animals. Olifiers *et al.* (2004) studied the relationship for 22 species of Neotropical marsupials, controlling for the possible effects of latitude and phylogeny. They found the triangular relationship described above and neither phylogeny nor latitude was important.

Bergmann's rule (Bergmann, 1847) states that average body sizes among populations of a single species or closely related species tend to decrease towards lower latitudes. As more research has emerged, the basis of this relationship has been increasingly questioned and this has been further substantiated by Hausdorf (2003), who demonstrated that, if phylogenetic effects are controlled for, neither latitudinal nor altitudinal patterns on body size could be found in populations of northwest European land snails.

### 4 Latitudinal species range and richness (diversity) relationships

Stevens (1989) introduced 'Rapoport's rule' that species geographic ranges demonstrated a decline in species range size from high to low latitudes. Rapoport (1982) originally suggested this idea using subspecies mammal data from North America and Stevens claimed to have shown the same relationship at the species level. The validity of the rule has been subsequently much debated and questioned (Gaston *et al.*, 1998; Gaston and Chown, 1999) and an increasing number of studies report the absence of or only weak evidence for the Rapoport effect across the full range of latitudes. A full discussion is given in Gaston (2003).

Relationships between species richness and latitude with highest richness in the tropics diminishing polewards have long been documented (Hawkins, 2001; Whittaker *et al.*, 2001; 2003; Gaston, 2003; Rosenzweig, 1995; 2003; Clarke and Crame, 2003). Various processes have been suggested to explain this pattern (Brown and Lomolino, 1998; Brown *et al.*, 2003b). Area, with greater land surface nearer the equator, encouraging greater diversity, has frequently been nominated as a key factor but is highly contentious (Rosenzweig, 2003). Geological and palaeoecological history is another (Clarke and Crame, 2003; Jablonski *et al.*, 2003), as is the historical and evolutionary perspective (Vogler and Ribera, 2003). Correlations with the obvious climatic-energetic gradient from equator to poles, which also links to productivity is yet another (Whittaker *et al.*, 2003; Rodriguero and Gorla, 2004) and latitudinal seasonal variability in temperature and precipitation still yet another (H-Acevedo and Currie, 2003). Debates over the relative contributions of these components are ongoing (Whittaker *et al.*, 2001; Hillebrand, 2004). Additionally, Koleff *et al.* (2003) tried to evaluate the further relationship between species spatial turnover and latitudinal gradients, which is thought to be related to higher levels of endemism at lower latitudes. Unfortunately,



problems of analysis in relation to the turnover indices employed mean that a clear picture and explanation has yet to emerge.

### 5 Macroecology and biological conservation

Gaston and Blackburn (2003b) and Gaston (2003) review the potential implications of macroecological research for conservation biology. All of the various macroscale relationships discussed above have been influenced, often extensively, by human activity. They describe how anthropogenic impacts have altered entry, exit and transformation rules that determine the arrival, extinction or change of species in particular situations. Species range contractions and extinctions, patterns of sizes and networks of protected areas, aliens and introduced species and, above all, the effects of climate change mean that all conservation scientists need to take account of macroecological theory and processes.

One example of an important implication of macroecology for conservation biology is that species abundance distributions are determined principally by the position of a community within the various independent geographical ranges of its species, rather than by the interactions of species with local environmental factors. Both siting of reserves and their management should be influenced by this but rarely are such macroecological factors taken into account in conservation planning (Gaston, 2003; McGill and Collins, 2003).

### 6 A metabolic theory of ecology

The most recent and exciting developments in macroecology relate to ideas of a metabolic theory of ecology. Brown *et al.* (2003a; 2004) and Enquist (2003) have clearly laid out the underlying principles and concepts. Metabolism involves the transformation of energy and materials by organisms in order to maintain life. As Brown *et al.* (2003a: 412) state: 'Understanding how individual organisms acquire metabolic resources from their environments and allocate them to maintenance,

growth and reproduction is key to explaining the emergent statistical behaviours of organisms in populations, communities and ecosystems.' Metabolic rate varies with body size, temperature and stoichiometry – the latter originally defined as the proportions of elements in chemical reactions but in this context broadened out to mean the quantities, or proportions of elements in different entities, for example, organisms or their environments (Brown *et al.*, 2004). Whole organism metabolic rate varies with the  $3/4$  power of body size and increases exponentially with temperature (Gillooly *et al.*, 2001). Allen *et al.* (2002) provide one example of how understanding of metabolic rate can be used to predict latitudinal species richness by demonstrating that the average energy flux of populations is temperature invariant and then deriving a model to predict quantitatively how species richness increases with increase in temperature.

The full implications of the theory have yet to be evaluated and a lively debate on the soundness of the theory and its potential applications has been published in an special edited Forum in the journal *Ecology* (Agrawal, 2004). Both further developments and demonstrations of the applicability of the theory are certain in the coming years, along with extensive further discussion and debate.

### III Conclusion – a unified theory for macroecology?

Beyond describing and explaining large-scale species distributions, macroecology is concerned with the search for general laws, theories and principles relating to the processes that underlie observed large-scale ecological spatial and temporal patterns. Within this, various researchers have tried to use theory to link together various different patterns that may be explained by a limited common set of processes. The result is usually termed a 'unified theory' and such theories are attractive because they demonstrate both elegance and parsimony (McGill

and Collins, 2003). Various 'unified theories' for macroecology have now been suggested (e.g., Hubbell, 2001; Hubbell and Lake, 2003; McGill and Collins, 2003; Nee, 2003; Brose *et al.*, 2004; Brown *et al.*, 2004). An emerging problem is how to choose between the different theories. Some theories may, of course be completely independent, since there are many different processes and mechanisms at work. Also, as Whittaker *et al.* (2001) and Willis and Whittaker (2002) have emphasized, the relevance of different unified theories may vary with spatial and temporal scale.

Further problems relate to the terminology of 'theories', 'laws' and 'rules'. Lawton (1999) points out that may so-called 'theories', 'laws' and 'rules' are not really so at all but are simply patterns, rather than conveying a clear message about process. At present, the evidence for a clear unified theory has yet to emerge but, as Lawton demonstrates, there is no doubt that very significant progress has been made in recent years and that the future holds exciting prospects for both biogeographers and ecologists.

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