



Macroecology: more than the division of food and space among species on continents

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Abstract: Macroecology is a big-picture, statistical approach to the study of ecology. By focusing on broadly occurring patterns and processes operating at large spatial and temporal scales and ignoring localized and fine-scaled details, macroecology aims to uncover general mechanisms operating at organism, population and ecosystem levels of organization. Although such an approach is evident in writings dating from the mid- to late 1800s, not until 1989 was the domain of macroecology clearly articulated. Since then there has been an exponential growth in publications employing a macroecological perspective. Here we (1) briefly review the history of macroecology, with emphasis on cultural, scientific and technological innovations that made this approach possible, (2) highlight current developments in the field, including its increasing linkages with biogeography and other disciplines, and (3) point to likely future directions. We also touch upon methodological, statistical and institutional challenges faced by this and other highly interdisciplinary approaches. Our review of macroecology is especially timely, since it has been 20 years since the term was coined and the seminal paper published.

Key words: biogeography, body size, metabolic theory, palaeoecology, range size, species abundance, species diversity.

I Introduction

Ecological systems typically contain many different kinds of organisms interacting in a myriad of ways with each other and their abiotic environment. Consequently, the

dynamics and structure of ecological systems are almost always highly complex. Such complexity is a challenge for modern science. While traditional ecology has made great strides in understanding various kinds of

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ecological interactions, it has been less successful at understanding the many connections between individuals, populations, communities and ecosystems and the emergent structures and dynamics generated by these interactions. Yet, understanding these linkages and their evolutionary history is imperative to solving emerging challenges posed by rapid rates of habitat fragmentation, loss of biodiversity and global climate change. In response, approaches that focus on broad patterns and seek to elucidate general processes in space and/or time are increasingly influential in ecology, evolution, systematics and palaeoecology (ie, Brown and Maurer, 1989; Blackburn and Gaston, 1994; Brown, 1995; Smith *et al.*, 1995; Gaston and Blackburn, 1996a; 1996b; 2000; Jablonski, 1997; Alroy, 1998; Enquist *et al.*, 1998; Roy *et al.*, 1998; Harvey and Rambaut, 2000; Erwin, 2007). One of these approaches, macroecology, explores the domain where ecology, biogeography, palaeobiology, and evolution overlap, and so it has the potential to forge synthetic links among these disciplines.

A macroecological approach to biology emphasizes describing and explaining processes that operate at regional to global spatial scales and decadal to millennial (or longer) temporal scales (Brown, 1995). The prefix 'macro' refers to both the broad and synthetic extent of the questions tackled as well as the fact that the approach derives much of its power from focusing on the emergent statistical properties of large numbers of ecological 'particles' (Brown, 1995). Statistical patterns that appear to be invariant across large scales suggest universal casual mechanisms operating at organism, population and ecosystem levels of organization (Brown and Maurer, 1989; Brown, 1995; Maurer, 1999; Gaston and Blackburn, 2000).

While macroecology is closely allied with biogeography, there are clear distinctions between the two. Most importantly, macroecology is an approach towards biology, rather than a discipline itself, so it necessarily

integrates divergent scientific methodologies, perspectives and disciplines (Brown and Maurer, 1989; Brown, 1995; 1999; Blackburn and Gaston, 2002). Moreover, while the main aims of biogeography are in understanding and describing patterns of biodiversity across space and time, macroecological approaches often focus on population or even individual level processes (eg, Damuth, 1981; West *et al.*, 1997; Enquist *et al.*, 1998; Belgrano *et al.*, 2002; Ernest *et al.*, 2003; Defeo and Cardoso, 2004). Because of the emphasis on identifying broad-based emergent patterns and processes, macroecologists necessarily 'stand back and take a sufficiently distant view so that the idiosyncratic details disappear and only the big, important features remain' (Brown, 1995:20). This is not an approach that lends itself to replicated experimental studies or standard statistical methodologies.

The past two decades have witnessed rapid expansion of macroecological research programmes, as demonstrated by an exponential increase in the number of published papers (Figure 1). Currently, macroecological publications are increasing by 34% per year, significantly higher than either the 14.6% for those in biogeography, or the 2.5% for scientific papers across all disciplines. Presumably this disproportionate increase in macroecological research reflects the growing realization that many complex biological problems are best tackled by adopting a new approach and using a different toolkit than employed in more traditional reductionist experimental science. Scientists involved in global change research, for example, have been particularly proactive in employing a macroecological perspective (eg, Kuhn *et al.*, 2008, and references therein). This led in 2006 to an international conference on the use of macroecology in global change research headed up by the recently established German Virtual Institute of Macroecology (www.macroecology.org). Similarly, the field of physical geography has embraced this approach to the extent that the flagship journal on macroecology (*Global Ecology and*

Biogeography: A Journal of Macroecology) has become the most influential in terms of ranking and impact factors (eg, Kent, 2007). The breadth of macroecological work has also grown tremendously; recent studies relate the temporal and spatial organization of numerous morphological, physiological, behavioural, ecological, evolutionary, phenological and phylogenetic traits among taxa as diverse as plants, birds, fish, mammals and

insects to past, ongoing and predicted future environmental fluctuations (Figure 2; Lyons, 2003; Hunt and Roy, 2006; Smith and Betancourt, 2006; Kerr *et al.*, 2007; Willis *et al.*, 2007; Kuhn *et al.*, 2008; Sekercioglu *et al.*, 2008).

Here, we describe the development of macroecology from earlier antecedents, briefly touch upon the importance of scientific and technological innovations that have

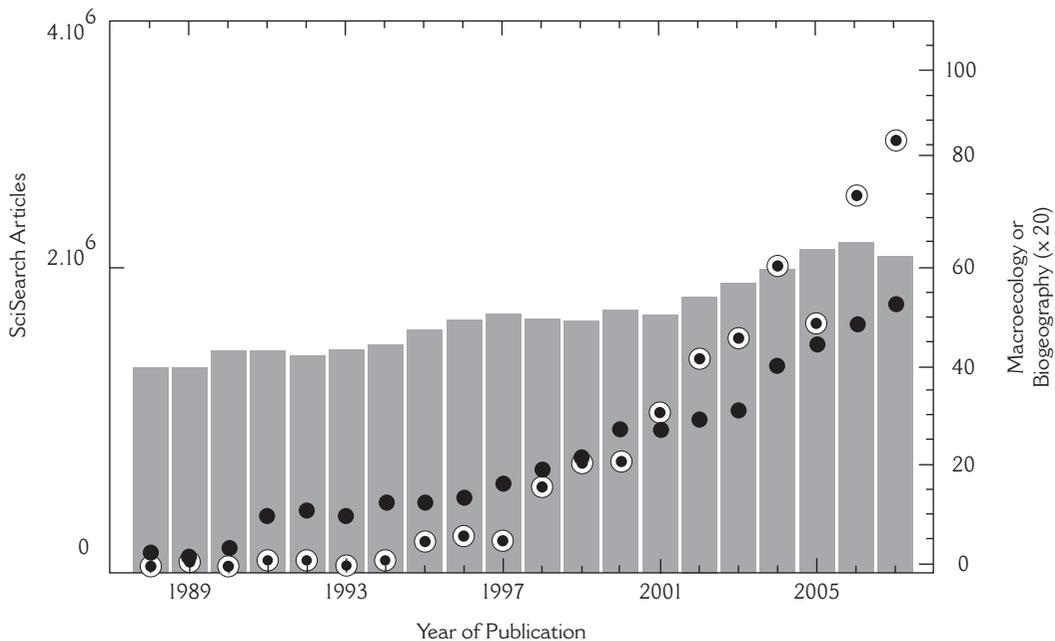


Figure 1 Rise in the number of published papers using macroecology (open circles with dots) or biogeography (filled circles) in the title, abstract or key words over the 20 years from 1988 to 2007. The term ‘macroecology’ was first coined by Brown and Maurer (1989). Data are taken from a search of over 21M records using ‘Search Plus v2.4’ – a comprehensive scientific search engine housed at Los Alamos National Laboratory. Shown also is the background rate of all papers indexed by this search engine over the same time period (grey bars). Although there has been a rise in all published works over the last 20 years, there have been significantly higher increases in papers containing biogeography and/or macroecology in their title, abstract or key words. Equations (log transformed): all SciSearch, $y = -14.84 + 0.011x$, $r^2 = 0.947$; all Biogeography, $y = -115.05 + 0.59x$, $r^2 = 0.92$; all macroecology, $y = -253.6 + 0.12x$, $r^2 = 0.93$; the 95% confidence intervals do not overlap for any of the equations. Note that, while both biogeography and macroecology have seen significant growth in publications, the slope for macroecology is significantly steeper and is best approximated by an exponential function (although a log transformed linear fit is used here for ease of comparison)

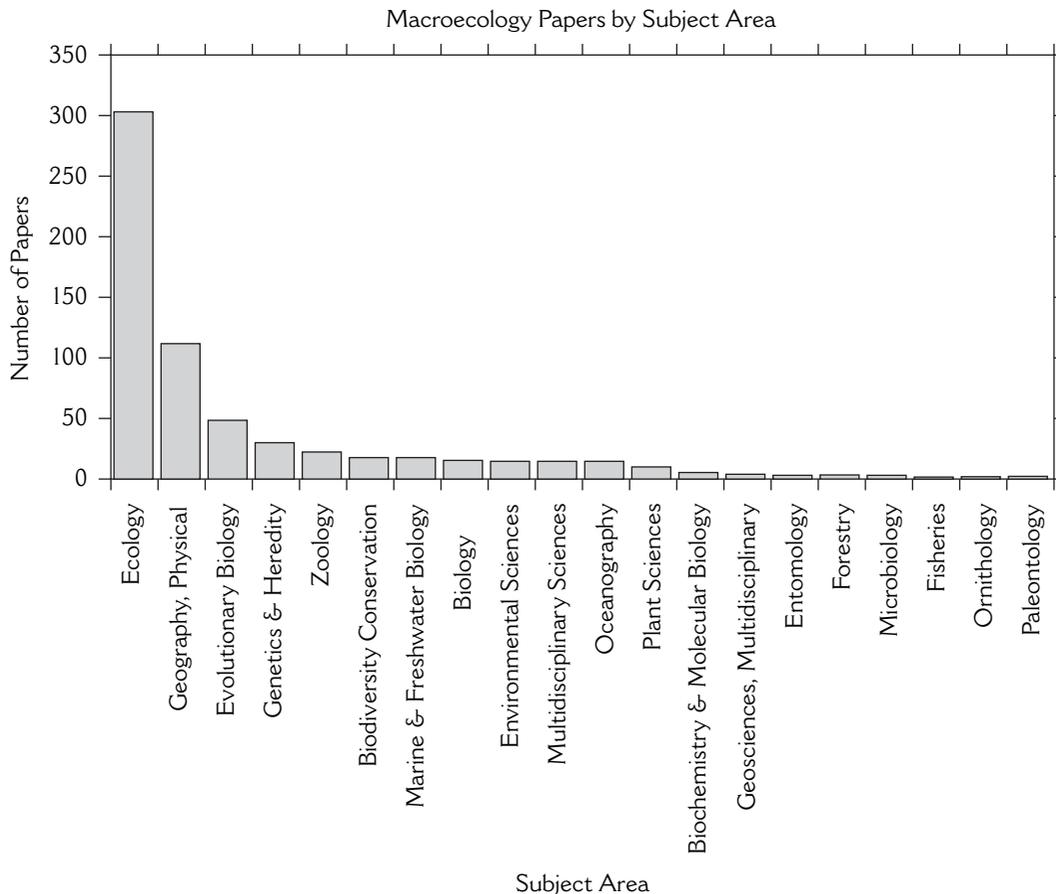


Figure 2 Subject areas of 383 papers using macroecology as a key word from 1994 to 2007. Data are taken from the ISI Web of Knowledge (http://apps.isiknowledge.com/WOS_GeneralSearch_input.do). Papers are sorted into subject categories as defined by the ISI Web of Knowledge; interdisciplinary papers may be counted more than once

made possible methodological advances, briefly highlight the current state of macroecological research, and speculate on future directions. Our aim is to provide a framework for understanding the current enthusiasm for macroecological approaches as well as to highlight some of the substantial scientific and statistical issues still facing broad-based synthetic studies.

II History of macroecology

Although first formalized in a series of papers by James Brown and Brian Maurer (1989; see

also Brown and Maurer, 1987; Brown, 1995), a macroecological perspective is clearly present in earlier writings. One of the first examples of this approach is evident from work published in the late 1800s. In an effort to understand whether the structure of natural fir forests differed from those of managed areas, de Liocourt (1898) measured and calculated the tree size distribution in three forests in Gérardmer (the Lorraine région of northeastern France). He found the number of tree stems declined exponentially with increasing diameter (Figure 3). The pattern

gave rise to a geometric series, which allowed predictions of the natural abundance of trees of particular size. While de Liocourt may have been one of the earliest to employ a macroecological perspective to understanding a biological problem, the approach he took is still typical of modern macroecology: identify a pattern that seems to be general and use that pattern to infer something about underlying principles of nature.

While some now classic macroecological patterns were first noted by the early biogeographers and natural historians (eg, species-area relationship – Watson, 1859; de Candolle, 1855; latitudinal gradient of species

richness – Wallace, 1878), many of the fundamental patterns were either discovered or seriously studied for the first time between 1900 and the 1960s. For example, seminal work was conducted during this time on the species-area distribution (Arrhenius, 1920; 1921; Willis, 1921; Williams, 1943), the relationship between body size and metabolic rate (Kleiber, 1932; Hemmingsen, 1960), the species abundance distribution (Fisher *et al.*, 1943; Williams, 1943; 1947; Preston, 1962), the latitudinal gradient (Fischer, 1960; Simpson, 1949) and the species-size distribution (Hutchinson and MacArthur, 1959). Many of these papers not only identified

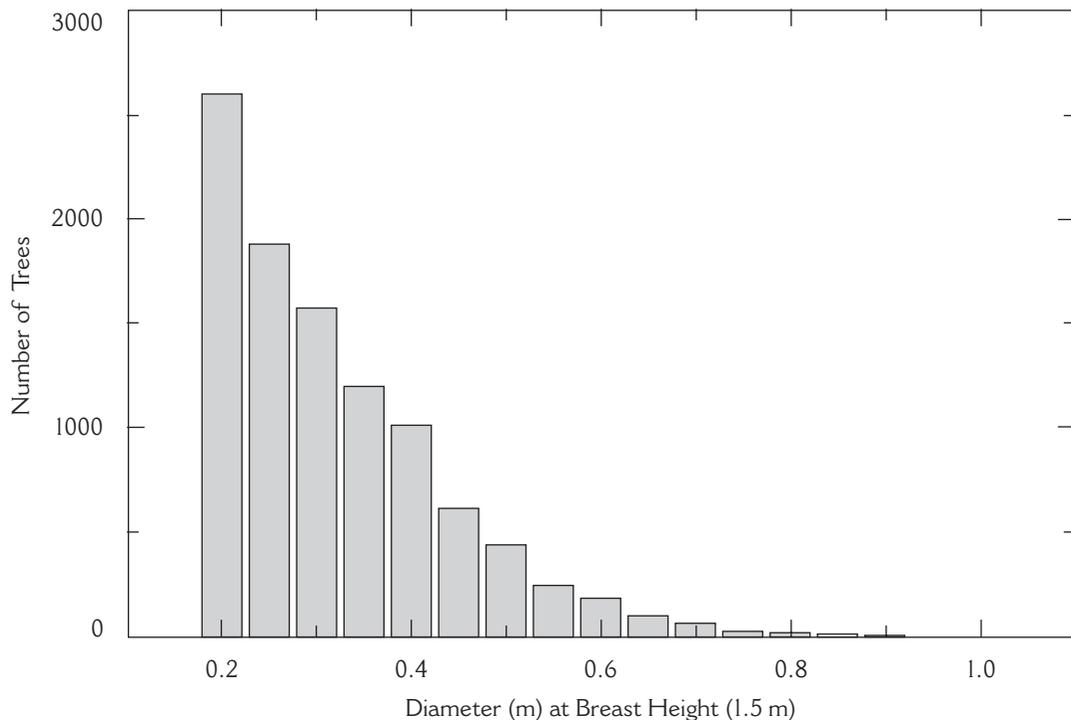


Figure 3 Natural distribution of fir trees of various size classes in uneven-aged forest stands in Gérardmer, northeastern France. Data are taken from tables published in de Liocourt (1898) and represent the mean of the three different sampled forests within the Lorraine région. Diameter of trees was measured at breast height (DBH; 1.5 m above the ground), and is given in metres. Note that the number of tree stems declines exponentially with increasing diameter of the tree. This study was one of the first to utilize a macroecological approach to ecological problems, and certainly the first to use it for conservation/management purposes

novel patterns, but also laid out methods, approaches and the basic philosophical reasoning for why these patterns provide important ecological insights.

It is interesting to speculate on why the early part of the twentieth century was such an important time for the development of the field. It seems reasonable that the proliferation of studies was related to developments in two of the essential components for macro-ecology: data and statistics. Until the early 1900s, a major focus in organismal biology was in collecting, documenting and classifying the natural world. By the 1900s, a large amount of data had accumulated on where species were found, characteristics of individual species, and taxonomic relationships among species. Since a macroecological approach is dependent on large data sets to obtain good statistical estimations of pattern and parameters, a critical level of data availability had to be reached before quantitative study of patterns became possible. It is also probably not a coincidence that many of the early macroecologists were also talented mathematicians and/or statisticians. For example, F.W. Preston, R.H. MacArthur, C.B. Williams and R.A. Fisher developed quantitative approaches for studying a variety of macroecological patterns; many of these are still in use today.

Despite its auspicious beginning, a macroecological approach fell from favour, beginning in the 1970s. In large part, this was probably due to a growing frustration with the more observational approach that made discerning the processes underlying patterns difficult. This frustration with inferring process from pattern is most clearly illustrated in the debates between Jared Diamond and Daniel Simberloff during the 1970s and 1980s. Diamond (1975), studying the distributions of bird species on the islands around New Guinea, reported the existence of 'chequerboard' patterns (ie, pairs of bird species that never co-occurred despite the fact that each species existed on islands that were easily

within dispersal distance of each other). He suggested that this pattern was created by strong competition between similar species, resulting in competitive exclusion. Connor and Simberloff (1979), using a null modelling approach, attempted to test whether these chequerboard patterns reflected an underlying competitive process or could simply result from the random placement of species among islands. Their conclusion was that random processes could explain the existence of chequerboard patterns without invoking strong competition between similar species. The resulting debate (Diamond and Gilpin, 1982; Connor and Simberloff, 1983; Gilpin and Diamond, 1984; Simberloff and Connor, 1984; see also Gotelli and McCabe, 2002) threw the search for process through the study of pattern into disarray. It also highlighted that the inferences obtained from observational studies are often weak (Tilman, 1989) and probably convinced many to focus instead on experimental manipulation where cause and effect are potentially easier to discern.

Despite the enthusiasm for, and widespread use of, experimental approaches in ecology, there are limits to the types of questions that can be addressed. Physical, logistical and financial constraints on experimental design and implementation severely restrict both the spatial and temporal scales that can be studied. Replicated experiments are often expensive to implement and maintain, resulting in predominantly short-term and small-scale approaches to biological questions (Tilman, 1989). Moreover, researchers tend to address questions where aspects of the system can be readily manipulated (eg, removal or addition of species, nutrient additions, habitat modifications). It is only in recent years that large-scale experiments have been initiated or even technologically possible (eg, Coale *et al.*, 1996; DeLucia *et al.*, 1999; Keller *et al.*, 2004).

Some biological phenomena, however, defy replication or experimental manipulation. Brown and Maurer (1989) highlighted the

use of what they termed a 'macroecological approach' to address such questions. Their first papers (Brown and Maurer, 1987; 1989; Maurer and Brown, 1988) focused on the pattern identified by Hutchinson and MacArthur (1959), the unimodal distribution of the number of species of different sizes at the continental to global scale. Brown and Maurer (1989) suggested that the assembly of continental biotas was the result of the interaction of evolutionary, physiological and ecological processes. Using a large data set of birds and mammals compiled for North America and a variety of multi-variate statistical analyses, they analysed the relationships between body mass, population density and geographical range. Specifically, their analysis predicted strong competition among species of similar size, higher extinction rates of larger species, and strong energetic constraints on smaller organisms. Brown and Maurer (1989) made two seminal contributions to development of macroecology. First, this paper demonstrated that there were still many interesting and fundamental unanswered questions about biological patterns that, because of their inherent spatial or temporal scales, could not be addressed through experimental manipulation. Second, Brown and Maurer (1989) demonstrated that observational studies do not necessarily result in weak inference if they are sufficiently rich in data and broad enough in scope to make multiple novel predictions about patterns and processes.

After Brown and Maurer (1989), macroecological approaches experienced a renaissance. This was at least partly because of advances in statistics and greater access to large accumulations of data. The development of the null modelling approach advocated by Connor and Simberloff (1979) continued through the 1980s, providing a new tool for assessing patterns (Gotelli and Graves, 1996). Clearly, the rapid increases in computing power and advent of personal computers and the web played an important role in macroecology's resurgence. As the amount of data employed in macroecological

research has increased and the statistics involved become more advanced, it has become practically impossible to conduct studies without the aid of computers. Many contemporary macroecological studies use data on literally thousands of species, individuals and/or locations (eg, Gaston and Blackburn, 1996a; Enquist *et al.*, 1998; Ernest *et al.*, 2003; Maurer *et al.*, 2004; Smith *et al.*, 2004; Orme *et al.*, 2006). The number of studies employing satellite imagery and climate-monitoring networks or other spatially explicit data to correlate with patterns occurring across space or through time has also increased (eg, Lyons, 2003; Kerkhoff and Enquist, 2006; Hurlbert and White, 2007; Sekercioglu *et al.*, 2008). Computers have allowed for better organization and availability of data; easily accessible electronic data sets are increasingly common. Examples include publicly available data sets on past and present geographical ranges (NatureServe, www.natureserve.org/; Faunmap, www.museum.state.il.us/research/faunmap/), body size (Dunning, 1993; Silva and Downing, 1995; Smith *et al.*, 2003), life history (Ernest, 2003), community composition (North American Breeding Bird Survey, www.mbr-pwrc.usgs.gov/bbs/), and numerous other integrated and searchable interfaces (eg, FishBase, www.fishbase.org/; the Paleobiology Database, <http://paleodb.org/cgi-bin/bridge.pl>; the Global Population Dynamics Database, www3.imperial.ac.uk/cpb/research/patternsandprocesses/gpdd). These easily accessible data sources have greatly facilitated the ability to ask questions across a large number of species, habitats and time periods. The combination of technological and statistical advances with ever more abundant, accessible and reliable data has allowed macroecologists both to discover new patterns and to test new hypotheses about old patterns.

III Current state of macroecology

Macroecology has grown rapidly since the term was first coined by Brown and Maurer (1989). Not only has the number

of papers increased disproportionately relative to related disciplines and to scientific publications overall (Figure 1), but the domain also has expanded as additional fields have incorporated macroecological approaches (Figure 2). Clearly, the power of macroecological perspectives to cross traditional boundaries and bridge disciplines has been embraced by the scientific community (Brown, 1999; Kent, 2007). Here we give a brief overview of the current state of macroecological research, and also discuss some applications of macroecological thinking, approaches and methodology to other fields.

1 Patterns of body size and energetics within and among species across space and time

Body size is arguably the most obvious and fundamental characteristic of an organism. Not only is it relatively easy to measure, but many important biological rates and times scale predictably with size (Peters, 1983; Calder, 1984). Consequently, much macroecological research has focused on patterns relating to body size. One of the most active and controversial areas of macroecological research in recent years concerns metabolic scaling (West *et al.*, 1997; 2002; 2003; Enquist *et al.*, 1998; Gillooly *et al.*, 2001; Agrawal, 2004). A $3/4$ power scaling relationship between metabolic rate and body size was first proposed by Max Kleiber (1932); both the pattern and the underlying mechanism have been the object of intense debate ever since. Much of the continuing controversy centres on whether the relationship is related to surface area, which would result in an exponent of $2/3$, or whether it reflects other physiological and/or structural constraints. In 1997, West *et al.* (1997) developed a general model based on the assumption that biological rates and times are limited by the rates at which energy can be supplied to cells. The original model was based on the mammalian cardiovascular system, but subsequent analyses extended the framework to plants, and potentially to organisms as diverse as microbes, invertebrates and other vertebrates

(Enquist *et al.*, 1998; West *et al.*, 2002; 2003). Although still controversial, this work demonstrates that scaling of whole-organism metabolic rate is reflected in the structural and functional properties of vascular systems. Specifically, fractal-like designs of surface areas and distribution networks allow diverse taxa of organisms to meet metabolic demands as body size increases. Among other things, the West *et al.* model predicted that whole-organism metabolic rate scaled as $\text{Mass}^{3/4}$. Expanding on this basic model, Gillooly *et al.* (2001) demonstrated that body size and temperature jointly regulate metabolic rate and many other biological rates and times. These models have subsequently been used to scale from individual metabolism to population and ecosystem-level properties, such as population density and species richness (Figure 4; Enquist *et al.*, 1998; 2003; Allen *et al.*, 2002; Banavar *et al.*, 2002; Belgrano *et al.*, 2002; Ernest *et al.*, 2003; Kerkhoff and Ballantyne, 2003; Kerkhoff and Enquist, 2006). There is still considerable controversy surrounding these models, ranging from the exact value of the exponents that characterize the relationships between physiological, life history and ecological attributes and body size (White and Seymour, 2003), to the ability of metabolic scaling relations to explain ecological rates and times (Algar *et al.*, 2007; Bokma, 2004).

Because so many traits that are of interest to ecologists scale with body size, much of macroecology is devoted to evaluating the form and strength of these relationships for different taxonomic groups and geographical regions (Figure 5). These include quantifying the relationship between body size and geographical range size (Gaston and Blackburn, 1996b; Brandle *et al.*, 2002; Willig *et al.*, 2003b; Murray and Hose, 2005; Rundle *et al.*, 2007), population density (Damuth, 1981; Pyron, 1999; Belgrano *et al.*, 2002; Defeo and Cardoso, 2004; Dinmore and Jennings, 2004; McClain, 2004; Hausdorf, 2007; Webb *et al.*, 2007), home range size (Kelt and van Vuren, 1999; 2001; Jetz *et al.*, 2004;

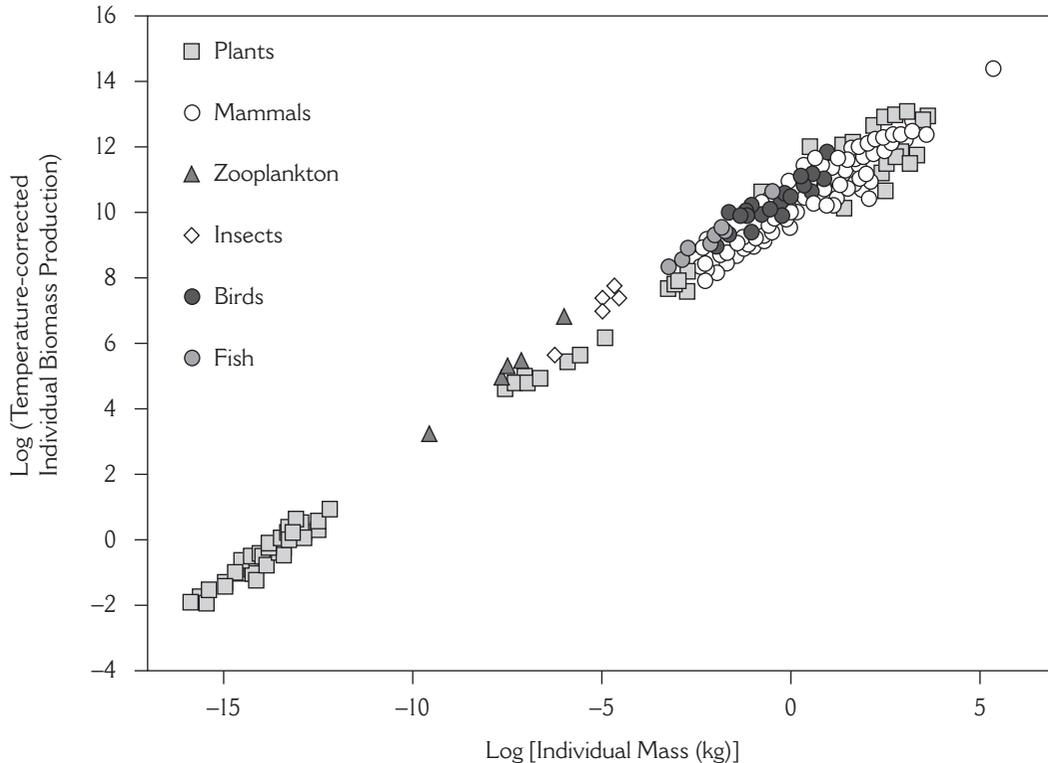


Figure 4 The relationship between body mass and whole organism biomass production, corrected for differences in organismal body temperature. The pattern is similar across plants, mammals, birds, fish, insects and zooplankton. The slope for all groups is statistically indistinguishable from the theoretical prediction of 0.75

Source: Redrawn from Ernest *et al.* (2003).

Hamilton *et al.*, 2007), as well as the relationships of these different variables with each other (Gaston and Blackburn, 1996a; Blackburn and Gaston, 2001; Fu *et al.*, 2004). In general, similar scaling relationships have been found for the many taxonomic groups examined. The relationship between body size and geographical range size is roughly triangle-shaped for most groups, for example, with large-bodied species having large geographical ranges and smaller-bodied species having a greater range of variation in geographical range size (Figure 5A; Brown, 1995). Other relationships are more tightly constrained so they can be described by

regression equations. For example, the log-log relationship between population density or abundance and body size tends to be linear in most groups, although often there is considerable residual unexplained variation (see Gaston, 2003, for a review).

Another thriving area of research in macroecology deals with the shapes of body-size distributions at various spatial, temporal and taxonomic scales (Figure 6). Brown and Nicoletto (1991) observed that the shapes of mammalian body-size distributions change with spatial scale in North America. At the continental scale, the body-size distribution is unimodal and right-skewed. As the spatial

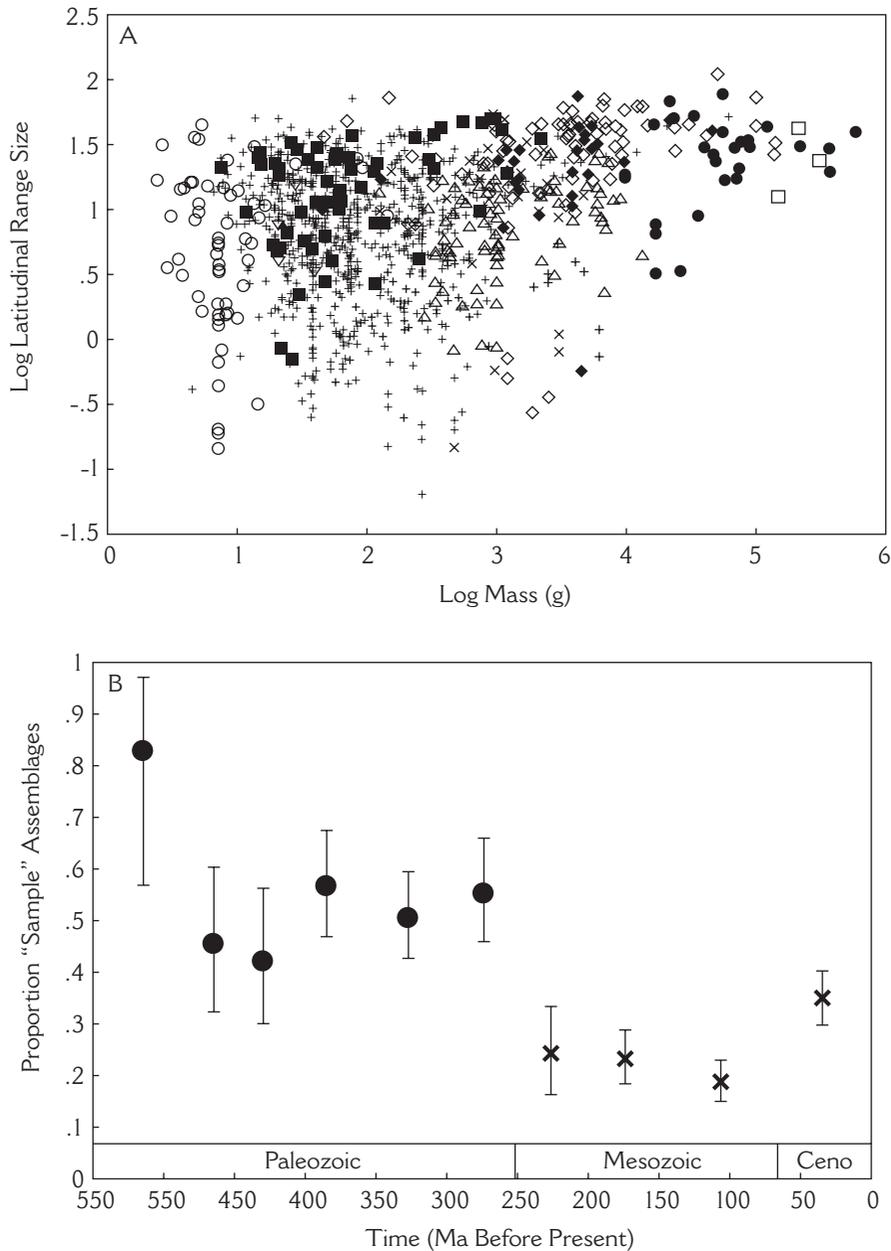


Figure 5 The relationship between body mass and various ecological metrics. (A) Log-transformed relationship between body mass and latitudinal range for all New World Mammals. Data for geographical range taken from Patterson *et al.* (2003); body mass from an updated version of Smith *et al.* (2003). Only modern species are shown. Symbols correspond to the different orders of mammals (closed circles: Artiodactyla; open diamonds: Carnivora; closed squares: Didelphimorphia; open circles: Insectivora; crosses: Lagomorpha; closed triangles: Microbiotheria; open upside-down triangle: Paucituberculata; open squares: Perissodactyla; open triangles: Primates, plus sign:

scale decreases, body-size distributions become progressively flatter until they are nearly uniform at the local community level. Similar patterns have subsequently been found in other vertebrate groups (Figure 6; Blackburn and Gaston, 1994; Brown, 1995; Maurer *et al.*, 2004). However, the unimodal right-skewed pattern is not universal. Some ectothermic vertebrates and invertebrate groups appear to demonstrate unimodal left-skewed body-size distributions (Poulin and Morand, 1997; Roy and Martien, 2001; Boback and Guyer, 2003). Moreover, the general flattening of the shape of the distribution with spatial scale may not occur in all locations or groups.

For example, mammalian communities in tropical forests in South America have more peaked distributions than those in other habitats (Marquet and Cofre, 1999; Bakker and Kelt, 2000) and the body-size distributions of bats are not flat at the local level across a wide range of latitudes (Willig *et al.*, 2008). Finally, there is some disagreement about whether patterns at the continental scale

are unimodal or multimodal (Cumming and Havlicek, 2002). Mammals have multimodal distributions on continents other than North America (Smith *et al.*, 2004) and prior to the late Pleistocene megafaunal extinction continental-size distributions of mammals on the major continents had a second mode of large-bodied species (Figure 6; Lyons *et al.*, 2004). Despite these seeming differences, there are gross similarities between the shapes of these distributions (Smith *et al.*, 2004) and exploration of the nuances between them are likely to shed light on the underlying ecological and evolutionary processes that give rise to them.

2 Abundance and distribution of species

Understanding the abundance and distribution of species is arguably one of the most fundamental goals of ecology. Macroecological studies offer multipronged approaches to questions relating to abundances and distribution. One active area of research involves documenting the relationships between patterns of species abundance and

Figure 5 (continued)

Rodentia; closed diamonds: Xenarthra). Describing the shape of these fundamental patterns is a major area of research in macroecology. For many taxonomic groups, the relationship between body mass and range size is triangular. This implies that small-bodied species can have either a small or broad geographical range, whereas large-bodied species can only have large ranges. This may be due to the packing of individual home ranges; larger animals require more space to meet metabolic requirements than do small ones. Note that for mammals this pattern is not simply due to turnover among the orders, but holds within orders as well. (B) Proportion of marine invertebrate communities with simple versus complex relative abundance distributions (RADs) over the Phanerozoic (figure redrawn from Wagner *et al.*, 2006). Relative abundance distributions have long been used in ecology to compare changes in community structure, but have been less frequently employed in palaeontology. Wagner *et al.* (2006) determined best-fit RADs for 1176 marine invertebrate communities spread over the last 540 Ma. As is clear from the figure, Palaeozoic communities are significantly best fit by RADs that imply simple ecological organization compared to post-Palaeozoic communities. This suggests that assembly rules for marine communities became more complicated after the end-Permian extinction. Symbols correspond to Palaeozoic (closed circles: 540 Ma to 250 Ma) and post-Palaeozoic (crosses: 250 Ma to present) communities. 'Error bars' represent one-unit support bars

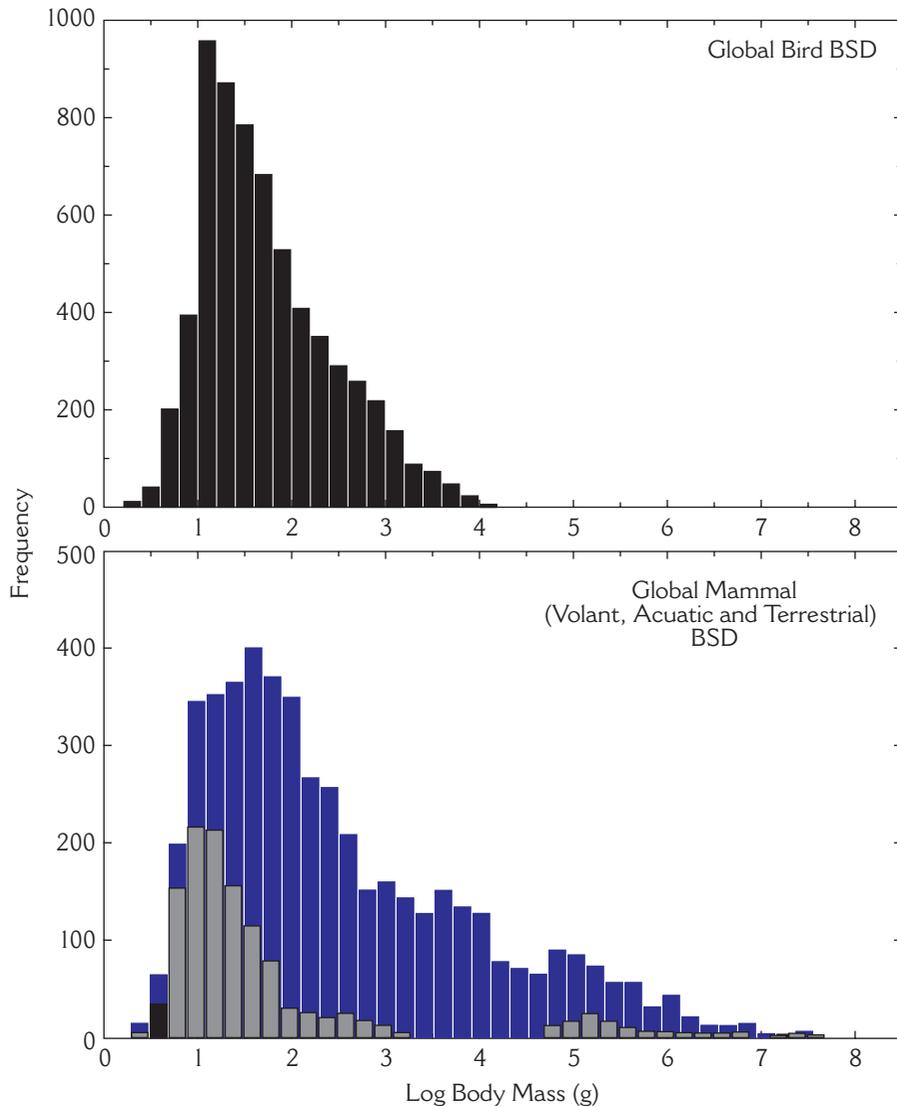


Figure 6 The global body-size distribution (BSD) for all birds (top) and mammals (bottom panel). Data for birds are taken from Dunning (1993) and for mammals from the updated version of Smith *et al.* (2003), which includes all late-Quaternary species. Volant mammals (eg, bats) are shown in black; aquatic mammals (seals, walrus, whales, etc) are shown in grey. Considerable research in macroecology has concentrated on describing the shape of these fundamental patterns (Brown and Nicoletto, 1991; Marquet and Cofre, 1999; Bakker and Kelt, 2000; Maurer *et al.*, 2004), which are remarkably constant across both geographical space and evolutionary time (Smith *et al.*, 2004). More recently there has been increased emphasis on understanding the constraints acting on body size (Smith *et al.*, 2004). Note that, for mammals at least, the distribution at the broadest scale is clearly multimodal; this is true even without the presence of large whales (grey shading)

other macroecological variables such as latitude, environmental heterogeneity, and continental versus island distribution for various taxonomic groups (Figure 5B; Gaston, 2003; Blackburn *et al.*, 2006). Another involves trying to explain the shapes of relative abundance distributions from a theoretical standpoint (eg, Hubbell, 2001; 2005; McGill, 2003a; McGill *et al.*, 2007; Nekola and Brown, 2007). Moreover, macroecological approaches are being applied to understand spatial variation in species abundances across landscapes or geographical ranges (eg, Murphy *et al.*, 2006; Hurlbert and White, 2007) as well as placement of geographical ranges across space (eg, Orme *et al.*, 2006). These studies have also led to growing recognition of the importance of spatial scale and the need for the development of new statistical approaches to deal with potential problems with spatial dependency and autocorrelation (Blackburn, 2004; Rahbek, 2005; Kent, 2007; McPherson and Jetz, 2007).

A particularly exciting and active area of research involves using macroecological approaches to understand the dynamics of ecological systems over time. These involve trying to understand the effects of anthropogenic environmental changes, ranging from human land use (Fisher and Frank, 2004; Gaston, 2004; Smith, 2006; Pautasso, 2007; Tittensor *et al.*, 2007; Webb *et al.*, 2007; White and Kerr, 2007; Wilson *et al.*, 2008) to ongoing global climate change (Kerr *et al.*, 2007; Kuhn *et al.*, 2008; Sekercioglu *et al.*, 2008). Additionally, palaeontologists are increasingly using macroecological techniques to understand the role of ecological processes in response to past environmental change. Such studies range from documenting macroecological patterns in the fossil record (MacFadden, 2006; Raia *et al.*, 2006; Butterfield, 2007; Huntley and Kowalewski, 2007) to using macroecological frameworks to understand macroevolutionary dynamics, including speciation, dispersal, extinction and diversification through time (Figures 5B

and 7; Hunt and Roy, 2006; Wagner *et al.*, 2006; Kiessling *et al.*, 2007; Willis *et al.*, 2007).

3 Assembly of biotas at multiple spatial and temporal scales

Understanding the processes that underlie species assembly is another area of research that has seen active growth in the number of studies using macroecological techniques. These range from simply documenting patterns of species diversity or abundance at different spatial or temporal scales (Frost *et al.*, 2004; Li *et al.*, 2006; Bruzgul and Hadly, 2007; Vanormelingen *et al.*, 2008) to evaluating changes in patterns of species traits of floras or faunas at multiple spatial scales (eg, body size; Brown and Nicoletto, 1991; Bakker and Kelt, 2000) to evaluating the relationship between species traits and species diversity at multiple spatial or temporal scales (Hamilton *et al.*, 2005; Swenson and Enquist, 2007; van der Veken *et al.*, 2007). A particularly productive area of current research is the application of Hubbell's (2001) neutral theory to macroecological questions (Maurer and McGill, 2004; Rangel and Diniz, 2005; Hu *et al.*, 2007). The growth in macroecological studies applying the neutral theory has occurred despite the controversy surrounding the theoretical underpinnings and empirical support for neutral theory (McGill, 2003b; McGill *et al.*, 2006; Pueyo *et al.*, 2007).

Macroecological research has brought the statistical rigour of large data sets and null hypotheses to understand better the assembly of biotas. For example, patterns such as checkerboards, nested subsets and morphological or taxonomic over- or underdispersion of species suggest hypotheses about the roles of processes such as interspecific competition in assembly of guilds and communities (Diamond, 1975; Kelt and Brown, 1999; Gotelli and McCabe, 2002). Other studies have applied allometric scaling and metabolic theory to higher levels of ecological organization (Kerkhoff and Enquist, 2006). A powerful starting point involves

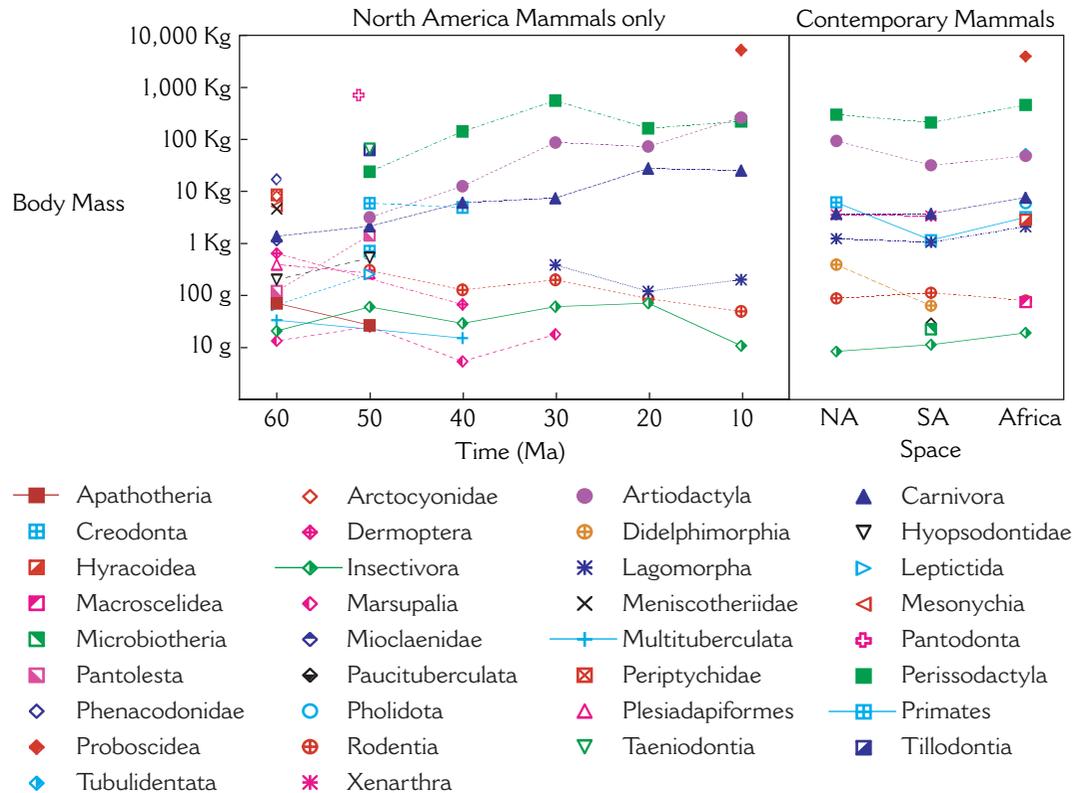


Figure 7 Body mass of mammalian orders and large families over evolutionary time (North America) and geographical space (North America, South America and Africa). The x-axis represents time on the left portion of the panel (depicted in 10 Ma slices for North America) or continent, depicted on the right portion of the panel; the y-axis, logarithmic mean of the body mass of species within the order or family. Many groups are represented over multiple time slices and/or different continents but, because of species turnover, few taxa persist for more than one datum. Note that modern values for North America and South America reflect the absence of most large megafauna (eg, members of Proboscidea and Perissodactyla) that went extinct at the early Holocene. Nonetheless, ordinal averages are strikingly similar over both time and space, suggesting the existence of body-size 'niches'; this is even more striking when these extinct megafauna are included (eg, Lyons *et al.*, 2004)

Source: Redrawn from Smith *et al.* (2004).

quantifying energy flow through communities using a macroecological framework. For example, White *et al.* (2004) demonstrated that community energy use by desert rodents remained relatively constant over a 30-year period, even though other community properties such as species composition and

body-size distributions changed dramatically as species colonized, went extinct, and varied in abundance in response to changes in climate and vegetation. However, the utility of an energetic approach to understanding communities is not restricted to the study of community assembly. Applications of

allometry and metabolic theory are also offering new insights into not only food web structure and dynamics (Hillebrand, 2004) but also carbon and nutrient flux in ecosystems (Enquist *et al.*, 2003; Allen *et al.*, 2005; Kerkhoff and Enquist, 2006). The application of a macroecological perspective to community ecology, in particular, has great potential for helping us understand how the structure and dynamics of communities in general may respond to a variety of anthropogenic perturbations challenging natural systems.

4 Applications to other fields

Macroecological approaches are often touted as being interdisciplinary and applicable across fields. A survey of the recent literature indicates that this claim has ample evidence (Figure 2). For example, macroecology is being increasingly applied to palaeontology and archaeology. Indeed, many palaeontologists now consider themselves macroecologists. However, other fields are increasingly adopting these perspectives and techniques as well. In particular, an increasing number of interdisciplinary marine studies are explicitly macroecological. These run the gamut from studies that investigate traditional macroecological patterns in the marine realm (McClain, 2004; Goodwin *et al.*, 2005; Beaugrand *et al.*, 2007; Helouet and Beaugrand, 2007) to those that document human impacts on marine biotas (Tittensor *et al.*, 2007). Others apply macroecological principles and analyses of metabolic scaling in the oceans to address questions about the allocation of energy and materials among marine organisms (Li, 2002; Finkel *et al.*, 2004; Cermeno *et al.*, 2006; Li *et al.*, 2006), the effect of body size and temperature on dispersal of planktonic larvae (O'Connor *et al.*, 2007; Duarte, 2007), the role of phytoplankton in the carbon cycle (Lopez-Urrutia *et al.*, 2006), and geographical patterns of genomic diversity in marine bacteria (Fuhrman *et al.*, 2008). Macroecological approaches have

even been applied to evaluating management and conservation decisions (Smith and Jones, 2007; Mora *et al.*, 2008). With the ongoing effects of anthropogenic change, these are likely to be expanding areas of research.

IV Future of macroecology

To date, macroecology has provided a number of useful insights into the structure and dynamics of complex ecological systems. Numerous studies have demonstrated the existence of fundamental macroecological patterns that hold across different taxonomic and functional groups and across both space and time (Figures 3–7; Damuth, 1981; Brown and Nicoletto, 1991; Gaston and Blackburn, 1996a; 1996b; Poulin and Morand, 1997; Marquet and Cofre, 1999; Pyron, 1999; Blackburn and Gaston, 2001; Roy and Martien, 2001; Jetz *et al.*, 2004; Maurer *et al.*, 2004; Murray and Hose, 2005; Li *et al.*, 2006; Hamilton *et al.*, 2007). In recent years, there has been an emphasis on shifting from descriptions of patterns to developing and testing hypotheses about ecological and evolutionary processes (West *et al.*, 1997; 2002; 2003; Poulin, 1997; Enquist *et al.*, 1998; Maurer and McGill, 2004; Blackburn and Gaston, 2006; Jablonski *et al.*, 2006; Lomolino *et al.*, 2006; Partel *et al.*, 2007). For example, one of the most puzzling and long-debated patterns in biology is the latitudinal gradient of species diversity. This pattern of increasing species diversity from the poles to the tropics is remarkably consistent across numerous marine and terrestrial taxa (plants, fish, birds, mammals, and many invertebrate groups) and has also persisted across much of both modern and deep time (Fischer, 1960; Pianka, 1966; Stehli, 1968; Stehli *et al.*, 1969; Kiestler, 1971; Horn and Allen, 1978; Crane and Lidgard, 1989; Rosenzweig, 1995; Willig *et al.*, 2003a; Hillebrand, 2004). Although a bewildering variety of mechanisms have been proposed (Wallace, 1878; Pianka, 1966; Buzas, 1972; Rohde, 1992; Willig *et al.*, 2003a; Brown and Sax, 2004; Wiens and Donoghue, 2004), there have been few if any

direct empirical and/or statistical tests. Using a macroecological approach, Jablonski *et al.* (2006) explicitly tested various evolutionary models with a global compilation of modern and deep time bivalves. They concluded that increased species diversity in the tropics is the result of both higher origination and persistence rates in this area relative to higher-latitude regions. This elegant study clearly demonstrates the utility of a macroecological perspective in disentangling complicated biological mechanisms.

Interestingly, this shift in emphasis from pattern to process was predicted by Brown 10 years ago:

There has been much progress in characterizing macroecological patterns and showing that they hold across different taxonomic and functional groups of organisms, kinds of environments, and geographical regions. There has been much less progress, however, in identifying the underlying mechanisms. The challenge for the future is to build and evaluate mechanistic models which can explain macroecological patterns in terms of established physical and biological principles. (Brown, 1999)

The continued development of mechanistic models to test patterns is likely to be an active and fertile area of future research.

A second major area of emphasis is likely to be the continued development of appropriate statistical tools and methodologies (Blackburn, 2004; Kent, 2007). Not only are macroecological studies conducted at larger geographical, taxonomic or temporal scales, but they often employ non-experimental data. Yet most modern statistical methods were developed specifically for traditional experimentally based science (eg, agriculture, domestic breeding programmes, biomedical, genetics) where the power of properly executed balanced experimental design can be used to test inferences. Macroecological approaches seldom meet the assumptions of such tests. Moreover, factors such as measurement scale are known to influence pattern (Burns,

2004; Rahbek, 2005; Pautasso, 2007). In response, macroecologists have turned to a variety of sampling, regression and hypothesis generation techniques such as the Neutral Theory, eigenvector-based spatial filtering, and others (Hubbell, 2001; 2005; Maurer and McGill, 2004; Diniz-Filho and Bini, 2005; Rangel and Diniz, 2005; Hu *et al.*, 2007). While these have proven useful in some areas of macroecology, particularly those involving spatial analysis of distributions (Kent, 2007), some methods remain controversial and/or of limited utility. Clearly, there remains an urgent need for the development of tools not only for macroecology, but also for many areas of conservation biology, palaeoecology or other disciplines employing large databases or 'natural experiments'.

Several research areas are likely to benefit greatly from the use of macroecological perspectives. Increasingly, palaeontology is embracing macroecological approaches. In many ways this is a natural development since the long time periods and large data sets that palaeontologists deal with naturally lend themselves to questions about broad-based pattern and process. Questions regarding potential tradeoffs over evolutionary time to vastly different environmental conditions are particularly relevant in light of concerns about anthropogenic climate change. Among ecologists there appears to be an increasing recognition of the importance of time in the structuring and functioning of ecological communities. This has been enhanced by recent workshops, working groups and symposia – for example, symposia at the 2007 Ecological Society of America (ESA) national meeting; working groups sponsored at the USA National Center for Ecological Analysis and Synthesis (NCEAS) and the USA National Evolutionary and Synthesis Center (NESCent); and a symposium at the 2008 joint meeting of the European Ecological Federation (EURECO) and the Ecological Society of Germany, Austria and Switzerland (GFÖ).

Another promising frontier is what might be called human macroecology. Humans

are among the most widely distributed, ecologically diverse and behaviourally unspecialized species that ever lived. Nevertheless, in their demography and life history, abundance and distribution, and interactions with abiotic environments and other organisms, humans are subject to the same basic principles and fundamental scientific laws as other organisms. Rigorous studies of human ecology have much to contribute to understanding the past history and present state of our own species, from the ancient spread of aboriginal humans out of Africa to colonize the entire globe, to the relatively recent development of agricultural, industrial and technological societies. Databases such as Binford (2001) and World Resources Institute (www.wri.org/ecosystems/data-maps-and-tools) lend themselves to the large-scale space-time perspectives and the statistical approaches of macroecology. Studies that have applied an explicitly macroecological framework have revealed patterns and processes that offer new insights into human ecology (eg, Collard and Foley, 2002; Moses and Brown, 2003; Hamilton *et al.*, 2007; Walker and Hamilton, 2008).

Computer and social scientists, physical scientists and others are also increasingly utilizing macroecological approaches. In particular, computer and social scientists use properties of biological systems to investigate how size and topology of networks may act to determine emergent system behaviour (Moses and Brown, 2003). Applications run the gamut from the energy and material distributional systems of roads and highways, oil pipelines and electric grids to information-processing networks within modern computer systems. Macroecology is one research programme that has had considerable success in understanding complex systems. Macroecologists have been using statistical techniques and mathematical models to reveal simple physical, chemical and biological principles that underlie the emergent structures and dynamics of populations, communities and ecosystems. Increasingly, these

approaches are being extended to study complex biological, social and technological systems.

1 Future challenges

Despite the enlightened call for interdisciplinary research to address the big scientific challenges of the twenty-first century, there remain considerable obstacles in the use of macroecological approaches to conduct synthetic work across traditional boundaries. First, in some areas the paucity of comprehensive data is still a major limitation hampering the development of research programmes that stretch across broad temporal or spatial scales. Collaborative networks such as the Palaeobiology Database (which modestly aims to bring together morphological, taxonomic and distributional information about 'the entire fossil record of plants and animals') are essential, but often go underfunded. Yet it is only by synthesizing emergent organismal and ecological data and patterns across multiple spatial, temporal and taxonomic scales that macroecologists will be able to identify commonalities and develop mechanistic models. Second, there remain sizable disciplinary hurdles. Scientists in different disciplines often have little opportunity for dialogue and the development of collaborative networks. Without a mechanism for promoting interpersonal interactions among scientists in relevant disciplines, it is difficult to overcome scientific and geographical isolationism and create productive working relationships. Cross-disciplinary collaboration is especially difficult, requiring persistent initiative and effective communication to make substantive progress. Without real incentives, it is much easier for both new and established scientists to keep doing safe, familiar research rather than to tackle challenging but risky new projects that require a substantial initial investment of time and effort. Third, there is still limited institutional and extramural support to span disciplinary and conceptual boundaries, let alone to coordinate research programmes

across multiple investigators, institutions and continents. This is exacerbated by the traditional structuring of universities and governmental funding agencies into physical and natural sciences, and into an organizational hierarchy of academic and administrative units, which tend to be physically separated and philosophically specialized. The progress made to date and the promising directions that macroecological research is taking suggest that these hurdles are worth navigating.

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