Chapter 1

Introduction: why macroecology?

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Introduction

For most of human history, most people's knowledge of the world was limited to the characteristics of, and events in, their immediate surroundings. This was the source of food, water and other resources required for their survival. It was also the home for those other people whose actions influenced their lives. For many, the events occurring amongst people in areas only a few tens of kilometres away from their home village or home range could be as irrelevant to their existence as events on Mars are to us today. A classic illustration is provided by the diversity of languages that have survived to modern times in the highlands of Papua New Guinea, the development of which is indicative of the lack of interaction between groups in some cases living in neighbouring valleys, separated only by a few kilometres (albeit of terrain that is very difficult to cross). Phenomena such as the weather, determined by processes acting over much larger scales, and hence unpredictable with only local knowledge, were often a source of awe and a spur for myth.

Slowly, however, people's awareness of the world beyond individual domains has expanded. Development of and improvements in agriculture raised the carrying capacity of the land, and allowed population growth. Expanding populations met and coalesced (not always voluntarily), with the result that seats of authority became increasingly removed from the majority of the populace. People's lives came to be influenced more and more by events happening further and further away.

The administration of any social or political system requires information to be communicated to its constituents. Larger systems require more efficient methods of transmission. In many societies, word of mouth was augmented or replaced by written communication, allowing greater volumes of information to be transmitted more reliably. However, the rate of dissemination was still limited by the necessity for the physical movement of literature. For example, Brown (1989) noted how, even before the invention of the telegraph, better communications infrastructure meant that news dissemination in North America had speeded up, so that by 1841 'news

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from Philadelphia covered the entire eastern seaboard, from Raleigh, North Carolina, to Pittsburgh, Pennsylvania, to Albany, New York, and north to Portland, Maine, within five days. Information from New York City was now arriving in nearly every city east of the Mississippi River within two weeks.' By modern standards, that is painfully slow. People corresponding between Britain and her furthest colonies could expect to wait several months for replies to their letters.

The invention of electronic communication has revolutionized the availability of information, a development that continues apace. Initially, telegraph and radio largely obviated the requirement for information to be disseminated by physical transport of documents. The scope of this revolution was broadened by the telephone, which personalized rapid communication. The need for physical document transport was reduced by the fax machine. Now, email allows manuscripts, figures and photographs to be transmitted across the world in seconds, rather than months. More powerful computers and capacious connections allow ever greater quantities of data to be processed and transmitted, and at ever greater speeds. As awareness of the world at large has expanded, so too have the means for communicating news of events of global import. This may now be widely available within minutes of an event's occurrence, or in real time (at least in those regions where sufficient freedom of the press is permitted). Events in New York City can now be watched as they happen.

The development of the science of ecology has been that of human society in microcosm. Since the early work of Elton (1927), the traditional focus has been on events and interactions occurring within a local community or species assemblage, and hence have concerned how ecological systems are structured by local-scale processes. Even today, the spatial extent of most ecological studies is on the order of square metres, rather than kilometres (Kareiva & Andersen 1988; May 1994; Baskin 1997; Lawton 1999; Gaston & Blackburn 2000). Studies are equally restricted in time, most being concerned with one or just a few seasons or years (Weatherhead 1986; Tilman 1989; Elliott 1994; Malmer 1994; Baskin 1997).

These points are well illustrated by the spatial and temporal scales with which papers appearing in the British Ecological Society publication *Journal of Animal Ecology* have been concerned (Figs 1.1 and 1.2). The number of papers published by the journal has grown ninefold from a low of 11 in 1945 (when matters other than ecology were of primary importance) to a high of 99 in 1999 (see also Shorrocks 1993). Most of that growth involves papers considering topics specifically addressing, or primarily relevant to, local ecological scales, or papers in the 'other' category, which principally comprise laboratory experiments and mathematical models (Fig. 1.1a). Studies specifically concerned with spatial scales larger than the local community (regional, national or biogeographical) have together shown some increase in number over time, particularly since the mid-1970s (see also Brown 1999). This growth over the past three decades is seen most clearly if the proportion of all studies in a given year is compared (Fig. 1.1b). However, also clear from Fig. 1.1b is that the growth is largely simply recouping ground lost in the 1950s and 1960s, which in Britain at least seem to have been the heyday of the local field study. Larger scale

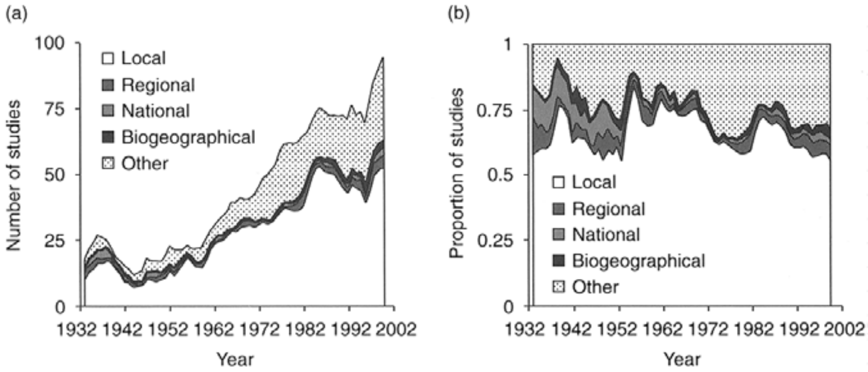

Figure 1.1 The number (a) and proportion (b) of papers published in *Journal of Animal Ecology* in each year between 1932 and 2001 (volumes 1–70, a total of 3042) that concern different spatial scales. The graphs have been smoothed using a 3-year running sum, and so the figures actually span the range 1933–2000. This classification does not include short communications (Comments or Forum papers). Studies were classified as 'local' if they were performed over restricted areas (e.g. at well-defined sites), or if they were performed at a few reasonably well separated sites but this separation was irrelevant to the aim of the study. 'Regional' studies were those concerning scales roughly equivalent to an English or American county, or a restricted part of a country. The 'national' scale refers to studies across regions roughly equivalent to whole countries, whereas 'biogeographical' studies consider multinational, continental or global scales. Studies that could not readily be assigned to any class in this scheme, or for which spatial scale was not relevant, were lumped into the 'other' category. These principally comprised papers reporting laboratory experiments or mathematical models, but also included reviews and some comparative analyses.

studies still represent a minority interest, if the composition of papers in *Journal of Animal Ecology* is a reasonable yardstick.

In terms of time, *Journal of Animal Ecology* has primarily published papers spanning relatively short temporal scales (Fig. 1.2). Most studies containing some field data tend to sample in only one to three different years. However, the number and proportion of longer term studies (4 years or more) published has increased over time, especially since the 1960s, such that these made up 37% of all papers published in the last three volumes. Studies of 7 years or more comprised one-quarter of all papers over these 3 years. Nevertheless, this general increase in temporal span should not be taken as indicative of a paradigm shift in ecological studies towards macroecological timescales. Rather, it represents the increasing availability of long-term data sets for local sites, as widespread recognition of the value of such data has resulted in ecologists extending their local studies as long as tenure, funding and longevity allow.

The increasing prevalence of long-term studies, albeit typically at small spatial scales, reflects an acknowledgement amongst ecologists of the importance of broader scale influences on local-scale communities, such as those mediated by the

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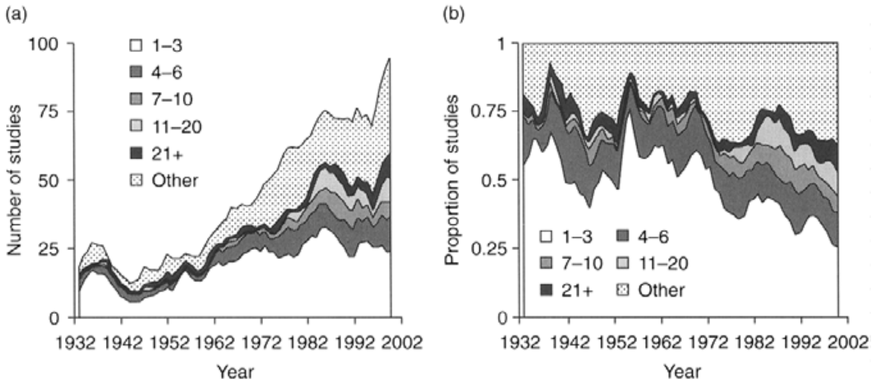

Figure 1.2 The number (a) and proportion (b) of papers published in *Journal of Animal Ecology* in each year between 1932 and 2001 (volumes 1–70, a total of 3042) that concern different temporal scales. The graphs have been smoothed using a 3-year running sum, and so the figures actually span the range 1933–2000. This classification does not include short communications (Comments or Forum papers). Studies were classified according to the number of calendar years in which field data used by the study were collected, or the range of years spanned by the data where this is relevant (e.g. data collected in 1982 and 1991 could be classified as a temporal scale of 2 years or 10 years, depending on whether or not the gap between the years was relevant for the aims of the study). Studies that could not readily be assigned to any class in this scheme, or for which temporal scale was not relevant, were lumped into the 'other' category. These principally comprised papers reporting laboratory experiments or mathematical models, but also included reviews and some comparative analyses.

weather and its temporal dynamics. However, significant effects of these outside influences often have been dismissed as 'unusual' events. For example, Weatherhead (1986) found that about 11% of studies in a sample of ecological journals reported unusual events, most of which referred to abiotic conditions. Unusual events were more frequent in shorter studies, suggesting that without the benefit of a longer perspective the importance of some events is overestimated. In other words, the effects of these outside events can be viewed as normal influences on local communities, which ecological studies need to incorporate, rather than events that disrupt the normal processes of ecological interactions.

At the same time as the attention of the general public was drawn towards the broad expanses of outer space, the early 1960s marked a rise in the attention paid by ecologists to the potential importance of larger scale influences on ecological systems. Publication in 1963 of the seminal paper on the equilibrium theory of insular zoogeography by MacArthur and Wilson (later generalized to the equilibrium theory of island biogeography: MacArthur & Wilson 1967) marked a milestone in this development. MacArthur & Wilson (1963, 1967) showed how the structure of ecological communities could be determined by immigration from a source pool of species, and local extinction within that community, with neither of these essential processes making reference to the identities of the species concerned. Although their model did incorporate biology, it showed that local-scale interactions were not required to generate realistic ecological communities. Similar processes were subsequently modelled by Levins (1969) to show how probabilistic immigration and extinction could determine the distribution of a species across an environment composed of discrete habitat patches.

Of course, large-scale patterns in ecological systems had been recognized long before the 1960s. For example, as early as 1807 Baron Alexander von Humboldt had noted that the variety of life increased from polar to tropical latitudes, describing what today is known as the latitudinal diversity gradient (Hawkins 2001). Arrhenius (1921) was apparently the first to point out that species richness generally increases with areal extent, and the observation that geographical range size may vary systematically with latitude was first made by Lutz (1921). These patterns ultimately must be the outcome of processes acting over large spatial and temporal scales — speciation, extinction and patterns of geographical range dynamics — albeit that local-scale interactions may influence and contribute. The importance of the insights of MacArthur and Wilson and others was to draw attention to the fact that the same large-scale processes also had the potential to drive local community structure. Indeed, they must, as local communities do not develop in isolation, but derive their constituents from the regional source pool. The composition of the pool constrains that of the local community.

Modern studies of large-scale effects in ecology arguably date to the beginning of the 1970s and publication of MacArthur's (1972) book *Geographical Ecology*, but growth since then has been slow. MacArthur's untimely death in that year may have been partly responsible for this, but the sheer difficulty of carrying out large-scale studies seems likely also to have contributed. Most such studies require large quantities of data, usually for multiple species occupying broad spatial extents. These data necessitate a massive effort and resources to collect, and are difficult to organize and analyse compared with those from studies of smaller spatial and temporal scale. All of these factors have counted against large-scale studies. In addition, the success of manipulative experiments in addressing ecological questions (e.g. Connell 1961; Paine 1966, 1974; Hairston 1989) seems to have developed a prejudice against the predominantly observational approaches that inevitably had to be adopted by ecologists interested in large-scale patterns and processes.

There is frequently a mismatch between what can be achieved with current levels of technological development, and what scientists would reasonably like to be able to achieve. This mismatch may be a spur for further such development, but equally it may be found that progress in one field of endeavour has serendipitous applications in others. So it has been with the information revolution and ecology. The rapid improvement in abilities to record, transmit, collate, store and process information provided by the development of digital computers, satellites and the internet has expanded the horizons of ecologists enormously. Many of the shackles that constrained the growth of large-scale ecology at the beginning of the 1970s have

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been broken. As a result, the past 15 years have witnessed a burgeoning of research into large-scale questions in ecology (for major reviews, see Hengeveld 1990; Ricklefs & Schluter 1993; Edwards *et al.* 1994; Gaston 1994; Brown 1995; Rosenzweig 1995; Maurer 1999; Gaston & Blackburn 2000), to the extent that a new term has been coined to help give this research coherence. This term is 'macroecology'.

What is macroecology?

Macroecology has been defined as concerned with understanding the division of food and space among species at large spatial (geographical) and temporal scales (Brown & Maurer 1989; Brown 1995). Perhaps more in keeping with definitions of ecology in general (e.g. Krebs 2001), it also can be regarded simply as being concerned with understanding the abundance and distribution of species at large spatial and temporal scales (Gaston & Blackburn 1999, 2000). As such, it can perhaps best be thought of as a field of study or a research programme. Brown *et al.* (this volume) emphasize the focus of macroecology on trying to describe and explain the statistical phenomenology of ecologically informative variables among large numbers of ecological 'particles', such as individuals within species or of species within communities. This approach to the study of ecology has a venerable history (e.g. Boycott 1919; Willis 1922; Hemmingsen 1934; Fisher *et al.* 1943; Preston 1948; Hutchinson & MacArthur 1959; MacArthur 1972). These definitions set out the principal aims of the macroecological research programme, which are to understand patterns in and determinants of the broad-scale distribution of life across the planet. Not explicit in these definitions are why such aims are sensible, nor what are their practical consequences.

The basis of the macroecological approach is to develop an understanding of ecological systems through the study of the properties of such systems in their entirety (MacArthur 1972; Brown 1995). This contrasts with the more traditional approach to ecology that seeks to develop such an understanding through reductionist study of the system's component parts (commonly referred to as a 'bottom-up' approach, as opposed to a 'top-down' one). Neither philosophy is inherently superior, albeit that the small-scale approach has to date predominated in ecology for the practical reasons described earlier. The macroecological view derives from the observation that complex systems, such as those of concern to ecologists, may exhibit properties or behaviours that arise from the interaction of their constituent parts, and so that are not evident in, or predictable from, knowledge of these parts alone (MacArthur 1972). Emergent properties make the behaviour of complex systems difficult to predict a priori. However, this difficulty can be circumvented easily by studying emergent properties directly. In ecology, this necessitates the large-scale approach that is the purlieu of macroecology.

Brown (1995) draws an analogy between the study of individual organisms or species and the study of gas molecules. It would be very hard, if not impossible, to understand the behaviour of gases from the study of individual molecules, although such studies would undoubtedly yield important insights. However, by studying the

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emergent statistical properties of large collections of molecules, scientists have discovered behaviours that are predictable enough to be enshrined as physical laws. This philosophy is not peculiar to macroecology. A complete understanding of most, if not all, scientific disciplines is likely to arise only by incorporating observations made from a range of viewpoints, or at a variety of scales (Dunbar 1995). The focus often changes as a field develops, and important gaps in knowledge are identified. In ecology, for example, the observation that species differ in their abundance led to attempts to describe the variation amongst large numbers of species, in studies that would today be termed macroecological (Fisher *et al.* 1943; Preston 1948, 1962). The descriptions initially were statistical, but mechanistic models of species–abundance distributions were developed subsequently (MacArthur 1960; Sugihara 1980; Tokeshi 1990, 1996; Hubbell 1997; Harte *et al.* 1999a). Models of species–abundance distributions have, in turn, resulted in studies aiming to validate assumptions or predictions of those models using small-scale data (e.g. Sugihara 1980; Harte *et al.* 1999b; Plotkin *et al.* 2000; Condit *et al.* 2002). Local ecological studies can be informed by macroecology, and vice versa. By following both small-scale 'bottom-up' and large-scale 'top-down' paths a better understanding has been reached than would have been derived from either approach alone. Both approaches are valid, and indeed necessary, tools for exploring the complexity of ecological systems.

The practical consequences of the macroecological approach are several-fold. Probably the most significant concern the methodology appropriate for answering questions in macroecology, statistical techniques, and the balance achieved between pattern and process in macroecological studies (Gaston & Blackburn 1999).

Methodology

Interest in large-scale questions largely precludes the use of manipulative experiments, as the scales involved are simply too great for most such experiments to be possible (practically or financially) or ethical. Manipulative experiments are not entirely precluded, however, as they can be used to address macroecological questions in systems where the manipulations are large scale for the organisms but not for the experimenter. Examples include the use of laboratory and field-based microcosms to investigate mechanisms underpinning interspecific relationships between abundance and distribution (Gaston & Warren 1997; Warren & Gaston 1997; Gonzalez *et al.* 1998). As manipulative experiments are probably the most powerful tool for differentiating between alternative hypotheses, such approaches are likely to become increasingly popular with macroecologists, albeit that the mechanisms structuring communities of organisms amenable to use in microcosms may be different to those for other groups, and issues of scaling between microcosms and geographical landscapes remain to be resolved (Peterson & Parker 1998).

Macroecological studies of larger bodied organisms typically rely on conclusions that can be drawn from natural experiments, the conceptually similar experiments in nature (Diamond 1986) or observational data (McArdle 1996). Natural experiments are changes in systems brought about by natural events, such as earthquakes and volcanic eruptions, whereas experiments in nature are changes in systems brought about as an intentional or accidental product of human activities, such as introductions of alien species. These are probably the only way in which experiments can be performed at the large temporal and spatial scales of concern to macroecologists. Their utility derives from their realism: unlike manipulative experiments, the study system is a natural entity. Thus, although natural experiments do not have the same discriminatory power as manipulative experiments, conclusions drawn from them may be more applicable to natural situations (Diamond 1986, 2001). Natural experiments have been a useful source of information on a variety of large-scale questions about ecological systems, such as those concerning extinction (e.g. Karr 1982; Pimm *et al.* 1988; Hinsley *et al.* 1995; Bellamy *et al.* 1996; Lomolino 1996; Manne *et al.* 1998; Spiller *et al.* 1998; Duncan & Young 2000; Terborgh *et al.* 2001) and invasion (Moulton & Pimm 1983, 1986; Moulton & Lockwood 1992; Thornton 1996; Veltman *et al.* 1996; Duncan 1997; Blackburn & Duncan 2001a, b).

In situations where neither manipulative nor natural experiments can be exploited, macroecologists generally must rely on observational data to generate and test hypotheses, and indeed this has been far and away the predominant approach to macroecological questions (see references in Gaston & Blackburn 2000). These data frequently derive from disparate unco-ordinated and unplanned sets of observations by multiple observers from different sites over a range of dates, so that their use must be tempered by caution if spurious and biased conclusions are to be avoided (Gotelli & Graves 1996; Blackburn & Gaston 1998, 2002). Observational data also generally lack the power to distinguish between similar hypotheses, which has lowered their respectability in recent years. Nevertheless, they form the foundation of most scientific disciplines, and with careful attention to their limitations can be valuable in hypothesis testing (McArdle 1996).

Statistical issues

The extent of the reliance of macroecology on unplanned natural experiments and observational data has two further consequences. First, because macroecological data usually lack controls, particular attention needs to be paid to the null hypothesis for any given data set or test. This issue has been discussed at length elsewhere in relation to macroecology (Gotelli & Graves 1996; Blackburn & Gaston 1998; Gaston & Blackburn 1999, 2000), although it is likely to remain a topic of fertile debate.

Second, a greater variety of statistical techniques generally need to be used to extract meaningful information from the raw data. When correctly formulated, controlled manipulative experiments allow the effects of all aspects of a system bar that under test to be held constant, so linking effects to causes (in practice, such an ideal situation can seldom be realized). The absence of controls in macroecological data can to some degree be compensated for by statistical approaches. For example, statistical null models can help identify significant features of macroecological data (Blackburn *et al.* 1990; Gotelli & Graves 1996; Gaston & Blackburn 1999; Colwell & Lees 2000; Gotelli 2000), and multivariate models can help factor out uncontrolled

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variation in natural systems (Mac Nally 1996; Thomson *et al.* 1996; Blackburn & Duncan 2001a). In many cases the data used by macroecologists, or the questions that they would wish to address, are difficult or impossible to analyse using traditional statistics (Blackburn & Gaston 1998). Macroecological studies frequently concern spatially or temporally explicit data, and so necessitate controls for associated autocorrelation (Lennon 2000; Lennon *et al.* 2001; Brewer & Gaston 2002). Similarly, because such studies often entail interspecific comparisons, as often required to elucidate the statistical phenomenology of ecologically informative variables among large numbers of ecological particles (Brown *et al.* this volume), autocorrelated responses of species owing to their shared phylogenetic inheritance need to be considered (Harvey & Pagel 1991; Harvey 1996; Blackburn & Gaston 1998; Gaston & Blackburn 2000). The techniques to allow these challenges to be met are only now being developed or discovered, their development motivated in part by the demands of the field (Purvis & Rambaut 1995; Carroll & Pearson 1998, 2000; Pagel 1999; Lennon 2000; Blackburn & Duncan 2001a).

Patterns and process

Finally, the constraints placed on macroecology by the methodological techniques available have had practical consequences for the theoretical development of the field. Whereas macroecological patterns are increasingly frequently reported, and hypotheses to explain them abound, unequivocal tests that link a given pattern to a specific process are relatively unusual. Although some hypotheses can be falsified for some systems (e.g. metapopulation dynamics cannot explain the positive abundance–occupancy relationship found for protist species across microcosms with no dispersal; Warren & Gaston 1997), it is much rarer for all bar one hypothesis to be falsified for any system (but see e.g. Gonzalez *et al.* 1998). It follows that understanding of process lags behind that of pattern in macroecology to a greater degree than in most other fields of ecology.

Gaston & Blackburn (1999) suggested two further reasons why an understanding of process in macroecology has been retarded, which are of particular relevance in the context of this symposium. First, different hypotheses of process may be rooted in different theoretical frameworks. For example, interspecific frequency distributions of body mass have been suggested to derive from speciation–extinction dynamics (Fowler & MacMahon 1982; Dial & Marzluff 1988; Maurer *et al.* 1992; Johst & Brandl 1997) or energetics (Brown *et al.* 1993; Maurer 1998), and abundance–occupancy relationships from resource usage (Brown 1984; Hanski *et al.* 1993; Gaston 1994) or population dynamics (Hanski *et al.* 1993; Holt *et al.* 1997). This means that hypothesized mechanisms may not be mutually exclusive, but instead represent different levels of explanation. Thus, the shape of a species–body-mass distribution must be explicable in terms of the differential speciation and extinction of species of different body size, but it may be patterns of energy usage that generate those differences in speciation and extinction rates. The multiplicity of frameworks means that macroecology currently lacks a central conceptual unification.

Second, even within a common theoretical framework, more than one mechanism may contribute to the observed form of a macroecological pattern. Ecology traditionally has been dominated by the search for single explanations for patterns, as typified by MacArthur & Connell's (1966) maxim that '(w)herever there is a widespread pattern, there is likely to be a general explanation which applies to the whole pattern'. However, although this view is both intrinsically appealing and satisfies Occam's razor, there is actually no necessary reason why it should be true. Indeed, given the complexity, variability and idiosyncrasy of ecological systems, it is perhaps more likely that a pattern that occurs across taxa, environments, or biogeographical regions may derive from the alignment of different contributory mechanisms, rather than the action of any given one (Wilson 1988; Warren & Gaston 1992; Blackburn & Gaston 1996; Lawton 1996; Gaston *et al.* 1997). The central question then becomes not which of any competing explanations is the correct one, but what is their relative importance, and when and where does this change. It also follows that identifying the mechanism underlying a given pattern in a given system does not mean that similar causal links apply to other systems (cf. Warren & Gaston 1997; Gonzalez *et al.* 1998). This considerably complicates the complete falsification of any macroecological hypothesis, unless that hypothesis is clearly context-specific.

Aims of this book

The combination of the need for a macroecological approach, the difficulty in implementing it, and the rapid development in the data and the tools available to do so, make this an exciting time for those involved in the field. Understanding is improving quickly. The present edited volume, the first dedicated to macroecology, brings together contributions from many of those at the forefront of these advances, with the primary goal of drawing out the divergent viewpoints on some of the major issues that macroecology has to address. The object here was not to expose these differences, as most have been well documented, but rather to seek to clarify the common ground they share, and thus to reveal some consensus about the shape of the natural world as viewed from a macroecological perspective.

The volume divides into eight main sections. In each of the first seven, two or more authors have been asked to address the same macroecological question from different viewpoints. None of these questions are novel, rather they for the most part reflect obvious characteristics of the natural world, such as the high diversity of species in the tropics, the predominance of small-bodied species, and the fact that most species are relatively rare. Nevertheless, answers to these questions are likely to prove central to a mature understanding of ecological systems, and so have captured the attention of macroecologists, and indeed ecologists more widely. They are also questions that have divided macroecological opinion, and so are ripe for the clarification and reconciliation that we hope that this volume will help advance.

The eighth and final section provides a series of statements about the relevance of the macroecological research programme. These statements show how macroecology is linked to, and can inform activities across, a broad swathe of environmental science. Given that we are part of the first generation in history that the