



Mammals on mountainsides: elevational patterns of diversity

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ABSTRACT

The four major papers in this special feature present and interpret data from field studies on the distributions and diversity of small mammals in elevational gradients on mountains in the Philippines, Borneo, southern Mexico and western United States. In the introductory paper, Lomolino places these studies in the context of historical, methodological and conceptual themes in contemporary biogeography. In this final paper, I focus on some important similarities and interesting differences among the four case studies. All of the studies provide evidence for the influence of ecological factors, such as climate, productivity and habitat heterogeneity, on mammalian divers-

ity. All also provide evidence for the influence of historical dispersal, extinction, and speciation events. Perhaps the most interesting result is the documentation of a frequent, but not universal, peak in species diversity at some elevation intermediate between the base and peak of a mountain. Efforts to understand the mechanistic basis for this pattern — and why it differs from the continuous decrease in diversity from the equator to the poles — promise to contribute to developing a general theoretical explanation for the major patterns of biodiversity on earth.

Key words biodiversity, ecological biogeography, environmental gradient, elevation, historical biogeography, mountain, species diversity.

INTRODUCTION

The last few decades have seen major advances in biogeography. Many factors have contributed: much better documentation of patterns of plant and animal distributions due to numerous field studies throughout the world; more and better information on the earth's abiotic template from surface measurements and remote sensing; vastly increased capability for compiling and analysing geographical data due to enhanced computer power and new statistical tools; greatly increased understanding of earth history due to empirical and theoretical advances in the earth sciences; and, perhaps most importantly, enormous progress in biogeography itself, using and synthesizing information from ecology, systematics and the earth sciences. Indeed, there have been true scientific revolutions in some of the areas mentioned above. The theory of plate tectonics, the reconstruction of phylogenies using molecular data and new conceptual paradigms, and the

accumulation of information on the deep sea offer excellent examples.

I believe that a similar revolution in biogeography is not far away. We have sufficient data and analytical capability to describe the major patterns of distribution of organisms, and to characterize quantitatively their relationships to contemporary and historical features of the earth's environment. What is needed now is to develop an appropriate body of general theory to explain and synthesize the empirical information. Some of the most general features of life on earth are the patterns of abundance, distribution and diversity of organisms in the earth's major environmental gradients, including those of latitude, elevation on land, depth in the sea, exposure in the intertidal and various kinds of physical disturbance. These patterns have been known for centuries, but their fundamental causes are still poorly understood. I believe that the understanding is imminent. We will soon have a general theoretical framework that will

explain the major features of the distributions of organisms with respect to the major patterns of physical geography.

Conceptual advances and syntheses are often stimulated by data from model empirical systems. This is certainly true in biogeography. Patterns of distribution of organisms on islands have served repeatedly as the inductive inspiration for new theory, from Darwin's (1859) theory of evolution by natural selection, to Mayr's (1942) ideas of speciation due to geographical isolation, to MacArthur & Wilson's (1967) theory of insular species diversity. Patterns of distribution on continents have similar potential, but the theoretical syntheses have been slower to emerge.

Distribution of terrestrial organisms along elevational gradients on mountains provides an excellent example. The papers in this special feature illustrate the state of the art. Lomolino's (2001) opening paper provides a historical and theoretical overview of biogeographical studies of elevational gradients. It identifies important methodological and conceptual issues that currently limit comparisons among empirical studies and hamper theoretical synthesis. The four following papers, by Heaney (2001) on the Philippines, Sánchez-Cordero (2001) on Oaxaca, Mexico and Md. Nor (2001) on Mt Kinabalu, Borneo, and Rickart (2001) on the Intermountain West of the United States provide case studies that document the distributions of mammals on mountainsides and evaluate the mechanisms that may have caused the observed patterns. As a result of these and other recent studies, we have more and better data than ever before on the abundance, distribution and diversity of different groups of organisms in different geographical regions, and on present and past variation in relevant environmental variables. Nevertheless, despite valiant efforts to relate the data to promising hypotheses about underlying mechanisms, theoretical unification remains elusive.

These concluding remarks attempt to provide some synthesis: to identify common themes and major differences among these and some related studies, and to compare them with empirical patterns and theoretical explanations for the geographical distributions of organisms in other gradients, particularly the latitudinal gradient from equator to poles. In so doing, I will try to clarify some of the conceptual issues, and to

give my own personal perspective on where we might look for additional theoretical unification.

THE CASE STUDIES OF MAMMALIAN DISTRIBUTIONS: COMMON FEATURES AND SYSTEM-SPECIFIC DIFFERENCES

The environmental setting

The earth is a complex place. It is not a perfect sphere with a uniform substrate and regular gradients of climate and other abiotic variables. Its surface is infinitely more complicated, so that no two geographically isolated places, and no two mountains, offer identical environmental conditions. Superimposed on this complex abiotic template are the even more complex patterns of animal, plant and microbe distributions. The biotic patterns are even more complicated than the abiotic patterns, in part because the distributions of organisms have been influenced by events of earth history and idiosyncracies of phylogenetic history as well as by contemporary environmental conditions, and in part because the distributions of organisms are influenced by interactions with other organisms.

Consider first the nature of the 'elevational gradient'. What is elevation a gradient of? By itself, elevation above sea level, like degree of latitude, means nothing to organisms. The correlated environmental variables, both past and present, abiotic and biotic, generate and maintain the patterns of abundance, distribution and diversity. A few environmental variables are closely correlated with elevation on all, or nearly all, mountains. Environmental temperature, atmospheric pressure and the partial pressures of biologically relevant gases, such as oxygen and carbon dioxide, tend to decrease relatively uniformly with increasing elevation, although even these variables are affected by local topography and weather. Because most mountains erode to produce gradually sloped, roughly conical land forms, land surface area also decreases relatively continuously with increasing elevation. A further consequence of uplifting and erosional processes is that tops of mountains tend to be more isolated than sites at lower elevations.

For other variables, however, the situation is more complicated. Precipitation and related

ecologically relevant variables, such as soil moisture and evapotranspiration, typically exhibit a non-linear relationship, with a peak at some intermediate elevation. Geological substrates reflect exposure of different strata due to uplift and erosion, and usually exhibit complicated, discontinuous patterns of variation. Differential erosion of substrates creates a heterogeneous topography of ridges, valleys, stream networks, and other features. The interacting influences of climate, topography and soil are primary determinants of plant distribution, so that variables such as vegetation structure and productivity also exhibit complex patterns on mountainsides. Finally, the attributes of biotic environments depend on the kinds of organisms that are present, and these in turn depend on complicated historical legacies: both the history of the landforms and climate that have influenced colonization, extinction and speciation of different taxa, and the history of the lineages of organisms that have constrained their traits, including their ecological interactions.

The four case studies illustrate these complicated patterns of environmental variation. None of the four environmental gradients are identical, so an important question is how similar or 'comparable' are they? Two of the case studies, Mt Kinabalu and the Philippines, are of islands, so the bases of the mountains are surrounded by water, and historical isolation by oceanic barriers has strongly influenced the composition of the flora and fauna. The other two case studies, Intermountain West and Oaxaca, represent continental settings, where the mountain slopes are less isolated from surrounding regions but the floras and faunas are probably no less influenced by historical events. In all cases, temperature declines with elevation, but precipitation and probably productivity are highest at intermediate elevations. This hump-shaped pattern is most conspicuous in Oaxaca and the Intermountain West, where low, sparse, shrubby vegetation occurs in the arid lowlands, and maximum productivity, most complicated vegetation structure, and highest plant species diversity occur in the more mesic woodlands and forests at higher elevations.

Distribution and diversity of mammals

It is difficult to make definitive comparisons among the patterns of mammalian distributions

reported in the four case studies. The studies had somewhat different designs and objectives, and were not intended to be directly comparable (also see Lomolino, 2001). Thus, Md. Nor's paper on Mt Kinabalu and Sánchez-Cordero's on Oaxaca report the results of original surveys on one or two mountainsides, respectively, whereas Heaney's analysis of several Philippine islands summarizes the results of decades of extensive field work by himself and colleagues, and Rickart's treatment of the many mountain ranges in the Intermountain region is based on nearly a century of systematic surveys and ecological studies in addition to his own work. The data from Mt Kinabalu and the Philippines span the entire range of elevations from sea level to the tops of the highest mountains, whereas those from Oaxaca and the Intermountain West start in the arid habitats at several hundred meters elevation and extend to the highest peaks. The studies also differ in the taxa of mammals considered (e.g. whether bats are included), kinds of data collected and analysed (e.g. whether abundance and trophic relationships are considered) and the kinds of ecological and historical phenomena emphasized (e.g. the relative emphasis on dispersal, extinction and speciation as opposed to contemporary ecological relationships).

Nevertheless, some common features and some equally important differences are apparent. All studies find a peak in species richness of non-volant mammals at intermediate elevations, but diversity of bats in Oaxaca and the Philippines declines continuously with elevation.

Because of correlation among variables, it is difficult to attribute the variation in the patterns of mammalian diversity to any single ecological variable. In general, species richness appears to vary positively with precipitation, and probably with other unmeasured variables such as evapotranspiration that index primary productivity (O'Brien, 1998; Whittaker & Field, 2000), food resource availability and structural heterogeneity of vegetation. In cases where total abundance of all species has been measured, it appears to be positively correlated with species richness. I note parenthetically that when considering the possible effect of productivity it is important to distinguish between primary production (rate of photosynthesis) and production of resources used directly by mammals, including not only

food, but also elements of habitat structure used for foraging, nesting or avoiding predation. It is the latter kind of productivity that should most directly influence mammalian diversity, and it may not be correlated precisely with primary production or surrogate variables such as actual or potential evapotranspiration. On the other hand, in none of the case studies does species richness appear to be correlated closely with area or temperature (or with total energy *sensu* Currie, 1991).

There are also some important differences among the case studies. Some ecological relationships appear to be region- or taxon-specific. The abundance of earthworms and the importance of these invertebrates in the diets of many terrestrial mammals, reported by Heaney in the Philippines, would not appear to hold for the other regions. Another difference already mentioned is the continuously increasing species diversity of bats with increasing elevation in Oaxaca, compared to the hump-shaped relationship for non-volant mammals.

It is even more difficult to generalize about the role of historic events in generating and maintaining the observed patterns of diversity. Three major classes of interrelated historical processes undoubtedly have influenced the relationship between mammal species richness and elevation patterns of diversity in all case studies. One is dispersal. Differing degrees and causes of historical and contemporary isolation of the habitats and mammalian taxa found at different elevations have resulted in important differences in dispersal and colonization. Particularly relevant are Pleistocene shifts in climate, sea level and vegetation that have periodically altered the habitat barriers and allowed interchange of non-volant mammals among islands and other isolated mountains. The second relevant historical process is extinction. Whereas dispersal facilitates the accumulation of diversity when barriers are temporarily reduced or absent, extinction tends to reduce diversity when the barriers are in place and populations are isolated. The third important historical process is differentiation and speciation. Long isolation of populations on different mountains or different habitats has often led to evolutionary differentiation, sometimes culminating in the formation of highly restricted endemic species. While these

three processes, dispersal, extinction and speciation, have played major roles in shaping the elevational variation in species diversity in all four mountain systems, the case studies suggest that in each region they have operated with different intensities and at different spatial and temporal scales, due in part to the influence of different ecological variables (e.g. Pleistocene shifts in sea level in the Philippines as opposed to shifts in climate and vegetation in the Inter-mountain West). The result has been a unique legacy of history on the patterns of elevational ranges, endemism and trophic and habitat specialization as documented in each case study.

AN EMERGING SYNTHESIS? PLACING THESE CASE STUDIES INTO A BROADER EMPIRICAL AND THEORETICAL FRAMEWORK

Ecological determinants: why does diversity peak at intermediate elevations?

As has been emphasized elsewhere (e.g. MacArthur, 1972; Brown, 1988; Rosenzweig, 1992, 1995; Brown & Lomolino, 1998), deterministic patterns of geographical variation in abundance, distribution and diversity must ultimately be explained by geographical variation in the earth's environment. Past environmental changes, especially in climate and geology, play key roles in generating the patterns of biodiversity, while variation in current environments is largely responsible for maintaining the patterns. So what are the ecological variables that are responsible for the observed patterns of mammalian diversity in these four elevational gradients? Can we generalize beyond these four case studies to make inferences about the ecological bases for geographical variation in diversity?

The most general finding of these case studies (except for bats in Oaxaca) is the peak in species richness at intermediate elevations. As pointed out by the authors (see citations in their papers and also Whittaker & Niering, 1975; Brown, 1988; Rhabek, 1995, 1997; Brown & Lomolino, 1998), this is a very common pattern. It has been reported for many taxa on many mountain slopes. Therefore, it is important to ask what may cause the general pattern, and also whether any insights may come from considering the exceptional cases

where diversity seemingly declines continuously with increasing elevation.

In any inductive analysis of patterns, it is often useful first to evaluate null hypotheses that might imply that a purported 'pattern' is actually the result of random processes. Colwell & Hurtt (1994) and Willig & Lyons (1998) have developed null models in which geographical ranges are placed at random, subject to certain constraints, into some specified interval corresponding to an elevational or latitudinal gradient. Results differ somewhat, depending on the details of the model and the nature of the constraints, but they often give a peak in diversity near the centre of the interval.

Additional insights come from simple deterministic graphical models of how species might be distributed in an environmental gradient without specifying precisely how their ranges are influenced by any particular variable or process (Fig. 1). I will consider three general cases, recognizing that there are many possible variations on these themes. One case occurs when species have specialized but partially overlapping requirements so that their ranges overlap somewhat but tend to be restricted to different parts of the gradient. This results in at least one peak in diversity at some intermediate point in the gradient, but the magnitude of the peak may be modest (Fig. 1a,b). The second case occurs when the species show a nested subset pattern of requirements and ranges. If the overlap is such that the species all occur at the centre of the gradient but they vary in how far they range toward the extremes, the result is again a peak in species richness at some intermediate position (Fig. 1c,d). The third case occurs when there is also a nested subset pattern of requirements and ranges, but the overlap occurs at one extreme of the environmental gradient, resulting in a continuous change in diversity with elevation (Fig. 1e,f).

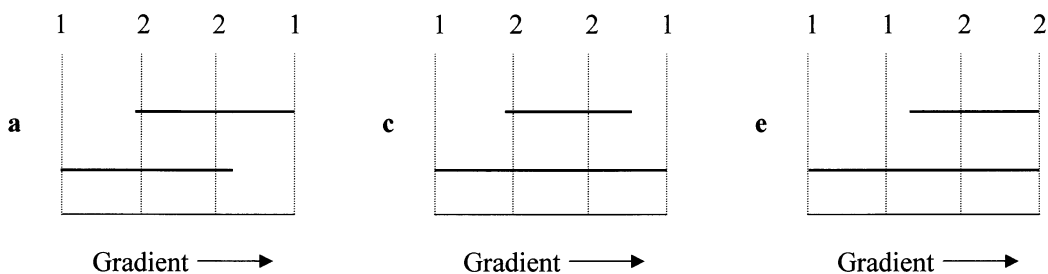
Both the strength and the weakness of the null and simple graphical models is the absence of specific mechanism. Because no particular ecological variable or process of range limitation is specified, the models are potentially very general and might apply to many situations. However, for the same reason their predictive and explanatory power is severely limited. They provide little basis for interpreting how specific ecological variables limit elevational ranges of

species or how many species co-exist in different parts of the gradient. Consequently, they are of limited utility in explaining why different taxa show different patterns or in understanding the quantitative patterns of range placement and species richness.

So why do peaks in diversity of non-volant mammals and many other organisms so frequently occur at intermediate elevations? I suspect that at least two ecological phenomena are responsible, and that their influence varies among taxa and geographical settings. First, when the elevational gradient spans a wide range of elevations from sea level to permanently ice-bound peaks, few if any species are able to tolerate the entire spectrum of environments and range throughout the gradient. Instead, species with elevationally limited ranges replace each other with some overlap along the mountainside. For the reason shown in Fig. 1a,b this results in at least one peak in diversity at some intermediate elevation. Secondly, if precipitation and consequently primary productivity also peak at an intermediate elevation and more productive sites can support more coexisting species (for mechanisms see MacArthur, 1972; Brown, 1988; Brown & Lomolino, 1998; references therein), this would cause a peak in diversity at the most productive elevation (one scenario consistent with this is shown in Fig. 1c,d). If the most productive part of the gradient corresponds with elevations where species with different requirements overlap in their ranges, then the two phenomena amplify each other, resulting in an even greater mid-elevation peak in diversity. This is almost certainly what happens on high mountains in desert regions: the species that can tolerate the hot arid lowlands cannot exist in the cold alpine environment and vice versa, but many species overlap at intermediate elevations where conditions are not so extreme. In addition, however, precipitation and productivity are substantially higher at intermediate elevations, and the greater abundance and variety of resources facilitates the co-existence of many species (e.g. Shreve, 1921; Whittaker & Niering, 1975; Brown & Lomolino, 1998).

I suspect that it is a relatively common phenomenon for peak productivity to coincide approximately with maximum overlap of ranges of elevationally restricted species. Desert mountains

Two species



Multiple species

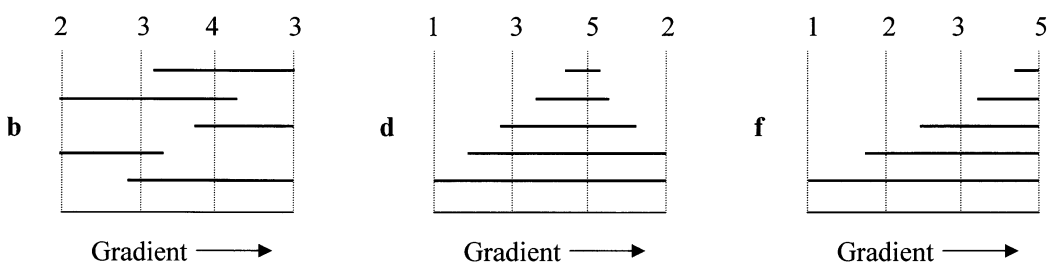


Fig. 1 Three kinds of simple deterministic graphical models that can generate patterns of species diversity within environmental gradients. Because the models contain no specific mechanisms, the gradient depicted on the x -axis could apply to elevation or any environmental variable. The ranges of the species along the gradient are depicted as horizontal lines, and the light vertical lines with numbers show hypothetical samples at different positions along the gradient and the resulting number of species. Two versions of each model are illustrated: the simplest, two-species case and a more complicated case for five species. a, b: The species have overlapping requirements and ranges, and some but not all species are able to occur at each extreme. This gives at least one peak in species richness at an intermediate position where ranges overlap. Note that if the x -axis represents disturbance or successional time, this model shows why there usually is a peak in diversity at some intermediate position in the gradient. c, d: The species have a nested subset pattern of requirements and ranges, such that the species all occur at some intermediate location, but they vary in how far they range toward the two extremes. This gives a peak in diversity at some intermediate location in the gradient. e, f: The species have a nested subset pattern of requirements and ranges, such that the species all occur at one extreme of the gradient. This gives a continuously increasing pattern of diversity.

provide only an extreme example of a much more widespread situation. Not all situations may be so simple, however. For example, there is no reason why the distribution of diversity with respect to elevation should always exhibit a single mode. It is easy to imagine that in some cases the combined influences of environmental conditions and historical events would cause two or more peaks of species richness along

the elevational gradient (see Heaney's discussion of the Philippines).

A peak in diversity near sea level and a continuous decline with increasing elevation was once thought to be the typical pattern (Brown & Gibson, 1983; Rhabek, 1995; Brown & Lomolino, 1998). We have two examples in these papers: in bats in Oaxaca and the Philippines (Heaney, 2001; Sánchez-Cordero 2001). Patterson *et al.*

(1996, 1998) find a similar pattern for bats, but not for birds or rodents, in the Andes. They present data to show that the elevational pattern of bat diversity reflects a nested subset pattern of elevational ranges (Fig. 1f; see Patterson *et al.*, 1996, 1998 for discussion of mechanisms). As new and better data on additional taxa and mountains accumulate, it will be interesting to compare the cases where diversity is highest near sea level as opposed to some higher elevation. Such comparative studies should contribute importantly to understanding the influences of ecological and historical processes on geographical patterns of diversity.

Historical influences on patterns of distribution and endemism

Elsewhere (Brown, 1995), I distinguish two different kinds of 'history': history of place and history of lineage. The history of place is earth history, the sequence of geological, climatic and other changes in past environments. The history of lineage is biological history, the sequence of changes in the genetics, morphology, physiology, behaviour and ecology of organisms due to phylogenetic ancestor–descendant relationships. Both kinds of history can have profound, long-lasting influences on biodiversity. The authors of the four case studies have provided cogent examples. There is abundant evidence from these case studies and other examples that historical environmental changes have influenced past dispersal, extinction, anagenetic differentiation and speciation processes. These changes in lineages in turn have influenced which species are present, how they are related to each other and what traits they possess. Present ecological relationships, including elevational ranges and geographical distributions, reflect a strong legacy of the histories of both place and lineage.

Unfortunately, it is difficult to synthesize these and other studies to provide satisfying generalities about the role of 'history'. Presumably this is at least in part because history is highly situation-contingent. The present distributions of species have been influenced by the features of past environments and the attributes of ancestral lineages. In part, too, the difficulty in making synthetic generalizations about historical influences may be because we have less experience

in erecting and evaluating historical hypotheses. Many studies in historical biogeography have focused on reconstructing the past distributions of single clades of closely related species, and few have tried to address broader patterns of diversity of entire faunas or floras.

Nevertheless, it may be possible to make some synthetic generalizations. Because of the general shapes of mountainous land forms, area decreases and isolation increases with increasing elevation. The reduced area might have resulted in high extinction rates. The increased isolation might have resulted in reduced dispersal and low rates of colonization. Both high extinction rates and low colonization rates would contribute to a decrease in species richness with increasing elevation. Additionally, increased isolation and reduced dispersal might have resulted in increased differentiation and higher endemism with increasing elevation, but these historical processes, by themselves and operating as hypothesized here, are inadequate to explain all of the observed patterns. They may account for the distribution of endemic taxa, the phylogenetic relationships within clades, and some features of diversity. To produce the peak of species richness at intermediate elevations, however, some other process is needed. It might be argued that the highest diversity is due to the influence of some intermediate value of area, isolation or both on historical patterns of dispersal, extinction and speciation. However, as suggested above, I think it is more likely that the co-existence of so many species at intermediate elevations can be attributed primarily to the special combination of ecological conditions.

CONCLUDING REMARKS: A BRIEF COMPARISON OF ELEVATIONAL AND LATITUDINAL GRADIENTS

One reason for studying elevational gradients is that the patterns of variation in both environmental conditions and biodiversity from base to peak of a tall mountain are similar in many respects to those from equator to pole. Producing a general theory for the pervasive latitudinal gradient of diversity remains one of the most vexing challenges of biogeography. There are many reasons why it is more practical to study the distributions of organisms on a single

mountainside (or several mountainsides within a geographical region) than along the entire latitudinal gradient: less travelling, sampling and taxonomic expertise is required; there is less confounding variation in ecological conditions, earth history and phylogenetic relationships; and mountains, like islands, are often 'replicated', allowing inferences from 'natural experiments'.

Mountainsides are not simply equator-to-pole transects in small, replicated, easily studied units. There are profound differences between elevational and latitudinal gradients. Both represent gradients of area, temperature and energy availability, but the seasonality of solar energy flux and related variables, such an important feature of the latitudinal gradient, is effectively held constant on a mountainside. Perhaps more importantly, as illustrated by these case studies, critical ecological variables, such as precipitation, productivity and structural complexity of vegetation, often show hump-shaped patterns in elevational gradients, but they decline more or less continuously from equator to pole. Further, because of the conical shapes of mountains, the influence of historical dispersal, extinction and speciation processes are quite different along elevational gradients on mountains than along latitudinal gradients on continents.

Armed with awareness of these important differences, comparisons of elevational and latitudinal gradients promise to contribute importantly to understanding patterns of biodiversity in both settings. Of particular interest is the widespread but not universal tendency for species richness to peak at some elevation intermediate between the base and peak of a mountain, but to decline relatively continuously from equator to pole. Although examples of the elevational pattern have been known for decades (e.g. Shreve, 1921; Whittaker & Niering, 1975), only recently has its widespread occurrence across different kinds of organisms and geographical regions been appreciated (e.g. Heaney & Rickart, 1990; Rhabek, 1995, 1997; Heaney, 2001). I think it is clear from these case studies and others cited in them that we do not yet have a single synthetic theory to explain this pattern. I think it is also clear, however, that we are making rapid advances. Considering that the general pattern itself was not appreciated just a decade ago (e.g. see Brown & Gibson, 1983; Brown, 1988), there

has been rapid progress, both in obtaining data on elevational distributions and related aspects of biodiversity, and in comparing these data to the predictions of mechanistic hypotheses.

I am optimistic, therefore, that within the next few years we will have general, widely accepted theoretical explanations for the common patterns of biodiversity in both elevational and latitudinal gradients. The explanations will necessarily be somewhat different because the patterns are different; but there will be many similarities, because the major geographical patterns of terrestrial biodiversity must ultimately depend on how the shape of the earth and the physical characteristics of its continents, oceans, climate, and land forms influence the distribution of energy, water and nutrients, and how the struggle of organisms to acquire these essential resources has influenced their abundance, distribution and diversity.

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