ELEVATIONAL TRENDS IN BIODIVERSITY

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GLOSSARY

alpha diversity Number of species within a restricted area, usually a small sample from a homogenous habitat.

beta diversity Change in species composition from one area to another.

ecotone An abrupt spatial transition from one community to another often caused by a change in environmental conditions or in the disappearance of a dominant species like the forest limit.

gamma diversity Total number of species within a large area or landscape encompassing a number of samples from different communities.

mid-domain effect A hypothesis based on random distribution of species ranges within a bounded domain resulting in maximum species richness in the middle of the domain.

source–sink dynamics Dynamics between populations that are net exporters of individuals and populations that are net importers of individuals.

ELEVATIONAL GRADIENTS in species diversity have great potential for increasing our knowledge about broad-scale diversity mechanisms. In this article, we describe the history of studies of elevational species-richness patterns from Grinnell and Whittaker until today. The observed elevational trend in species varies among groups of organisms and from area to area. The most commonly observed patterns are decreasing richness with increasing elevation and a humped pattern with a richness peak at intermediate elevations. We discuss some hypotheses which may be important in shaping the richness trends, including productivity/energy, mid-domain effect (MDE), source–sink dynamics, species–area relationships, heterogeneity, and history.

I. INTRODUCTION

When walking along an elevational gradient we see many features change as we walk upwards passing through various life zones. At its most dramatic it may change from a dense tropical forest that is packed with visible biological life to the snow-capped tops with no sign of life. When comparing these extremes it is obvious that species richness is lower at the extreme mountaintops than in the lowlands. The striking changes in climate, plant communities, and faunal assemblages with increasing elevation have led to the formulation of many of the most widely accepted ecological concepts, including niche theory, life zones,

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community assembly, and insular biogeography. The interest in elevational patterns, particularly in species richness, has fluctuated over the last 100 years, but has greatly increased over the last decade as a result of the increasing interest in broad-scale patterns of biodiversity. Rigorous quantification of elevational species-richness patterns from different parts of the world may prove to be the key to a much-needed understanding of broad-scale diversity mechanisms.

II. HISTORY OF ELEVATIONAL STUDIES

It has probably always been acknowledged, and it was clearly noted by the nineteenth century naturalists, that diversity of plants and animals was higher in the lowlands than at the mountaintops. Willdenow, von Humboldt, Darwin, and Wallace made detailed observations along altitude and noted that the stature and diversity behaved in the same way along altitude and latitude (Lomolino, 2001). In fact, Linne and Willdenow went further and actually explained the latitudinal distribution of species to be a result of elevational distributions during the Great Flood (Lomolino, 2001).

Among the first rigorous quantitative descriptions of elevational species-richness patterns were works by Joseph Grinnell, Robert H. Whittaker, and colleagues (Grinnell and Storer, 1924; Whittaker, 1952, 1960, 1967; Whittaker and Niering, 1965). Grinnell, known for coining the niche concept, detailed species distributions, abundance patterns, and range limits of vertebrates along an elevational transect in the Yosemite region of the Sierra Nevadas, CA, USA (1924). His study emphasized that the "amplitude of the general environment—the number and extent of distinct ecologic niches it compasses—determines the richness of the fauna, both as regards number of species, and the number of the individuals to the unit of area representing each species." While Grinnell used elevational distribution patterns to understand niches and richness patterns, Whittaker undertook elevational gradient studies in the Great Smoky Mountains (insects; 1952), Siskiyou Mountains (plants; 1960), and Santa Catalina Mountains (plants; Whittaker and Niering, 1965) to tease apart important potential climatic drivers of species richness and abundance (e.g., water availability, soil type, and temperature), and to determine the cohesiveness of communities.

Whittaker's elevational studies tested community cohesion by contrasting the support for the two main hypotheses: Gleasonian continuum hypothesis versus Clementsian discontinuity hypothesis. The discontinuity hypothesis proposes that groups of species have similar distribution along an environmental gradient with more or less clearly defined transition to another group of species, that is, that the community actually behaved as a superorganism with respect to the environment. The continuum hypothesis proposes that the individual species are distributed independently from each other, and that centers and boundaries of species populations are scattered along the environmental gradient. With numerous studies, using elevational gradients as their test system, Whittaker and colleagues found that species tended to have independent range boundaries providing evidence against the discontinuity hypothesis and supporting the continuum hypothesis. These studies had an enormous impact on vegetation ecology, sparkled gradient analyses, and ignited the use and development of ordination techniques and related statistical methods in ecology.

At the same time as discussing the cohesiveness of communities, Whittaker and colleagues detailed both monotonically decreasing species richness with increasing elevation and humped pattern with maximum species richness at intermediate elevations (e.g., Fig. 1a). Grinnell and Storer (1924) determined that each group of vertebrates (bats, rodents, breeding birds, amphibians, and reptiles) exhibited a humped richness pattern with the highest species richness between 1000 and 1300 m. One important conclusion is that richness patterns found in Whittaker's studies differed among species groups (e.g., trees, bushes, and herbs; flies, beetles, and grasshoppers), whereas different vertebrate groups in Grinnell's studies showed consistent diversity trends with elevation. The combination of studying patterns in species richness and gradient analyses naturally lead to a way of quantifying the degree of change in composition of communities along a gradient, which Whittaker (1960) termed beta diversity.

After Whittaker, most attention to broad-scale patterns in diversity was focused on latitudinal gradients. This continued until the seminal work of John Terborgh on bird communities along an elevational transect in the Peruvian Andes (e.g., Terborgh, 1971, 1977, 1985). Terborgh's widely cited bird study detailed strongly decreasing richness with increasing elevation and showed support for the importance of habitat complexity, competition, and ecotones in bird diversity patterns. Thereafter, decreasing diversity along elevational clines became the accepted and assumed pattern for all taxonomic groups, that is, the elevational pattern mirrored the latitudinal pattern of diversity (e.g., Brown and Lomolino, 1998). As time passed,

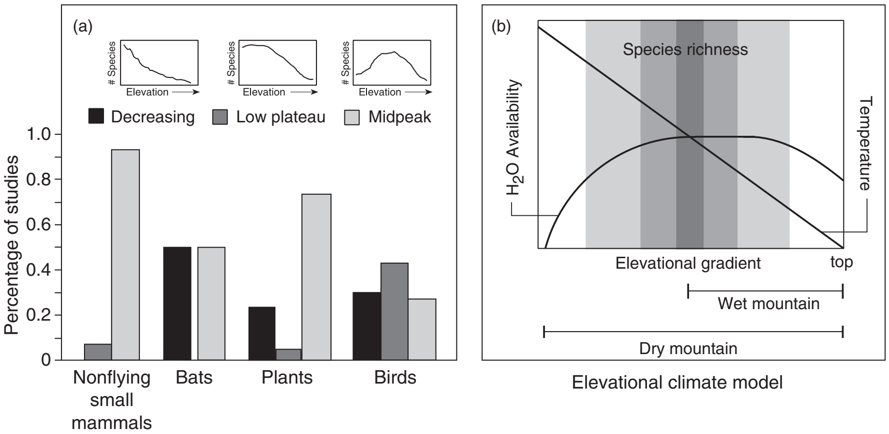

FIGURE 1 (a) The percentage of each of the three main elevational richness patterns demonstrated in the robust, informative montane gradients across the globe: nonflying small mammals (McCain, 2005); bats (McCain, 2007); plants (from Rahbek 2005, fig. 3f; plant percentages rescaled to include only these three diversity patterns), and the preliminary results for birds. (b) Generalized climatic model for elevational species richness, incorporating a linearly decreasing temperature gradient and a unimodal water availability gradient. Species richness is depicted in gray tones with darker indicating more species. The placements of generalized wet and dry montane gradients are shown below the *x*-axis (e.g., McCain, 2007). Adapted from McCain (2007), with permission.

the humped elevational patterns of Grinnell and Whittaker were forgotten, although their contributions on niches, community cohesiveness, and gradient analysis were not. Rahbek (1995) began to question the pervasiveness of the decreasing diversity pattern, which he claimed was based on very few studies that had serious sampling biases and called for more rigorous studies on elevational patterns. He presented a preliminary overview of elevational diversity patterns, and found more support for humped richness patterns with the highest richness at intermediate elevations than decreasing patterns. After Rahbek's study in 1995, the interest in elevational patterns in species richness has increased enormously. Today, elevational gradient studies are often motivated by increasing our knowledge about broad-scale patterns in diversity and the search for global drivers of biodiversity that are so urgently needed for conservation efforts worldwide. As noted by Grinnell and Whittaker, and repeated recently by Lomolino (2001) and Brown (2001), the elevational gradient is ideal for studying on broad-scale distribution of species and species richness.

III. OBSERVED PATTERNS AND WAYS OF QUANTIFYING PATTERNS

Two types of data are used to quantify the elevational pattern in species richness. Alpha diversity studies use local field sampling of plots along a transect usually on one mountain slope, preferably with equal sampling effort at each elevational band. Alternatively, gamma-diversity studies use regional data from previously collected specimens and field records for an entire mountain or mountainous region. Such regional data are often readily available and summarized in flora and faunas from mountainous areas around the world.

Unlike other broad-scale gradients, field sampling is feasible for elevational transects and together with appropriate statistical methods can give a robust richness estimate. When using museum or historical data the observed pattern may be very sensitive to the intensity of sampling. One common way to account for sampling intensity is to assume that each species is present at all elevations between the upper and lower elevation of observation (interpolation). However, interpolation can create an artificial hump in species richness along the elevational gradient if sampling is incomplete (Grytnes and Vetaas, 2002). If more detailed specimen information is available, uneven sampling may be accounted for by using rarefaction or extrapolation (see Magurran, 2004); without such information error simulations can test for pattern robustness (e.g., McCain, 2007).

Rahbek (2005) conducted an overview of elevational richness patterns from the literature. The majority of these studies examined plants and he demonstrated that almost 50% of these studies found a humped pattern, and around 25% had a monotonic decrease with elevation. The fraction of hump-shaped patterns increased to around 70% after excluding studies that did not consider the whole gradient (Fig. 1a, plants). Rahbek's study also demonstrated the importance of scale, for example, a hump-shaped pattern is more common if a single transect is studied (i.e., alpha diversity) than if the pattern is studied on a whole mountain range (i.e., gamma diversity).

McCain has begun a series of global meta-analyses on elevational richness patterns among taxonomic groups from published studies. These and previous analyses clearly show that the observed pattern depends on the organism studied and the local climatic conditions (Fig. 1a; McCain, 2005, 2007, in press; Rahbek, 2005). Nonflying small mammals (rodents, shrews, and marsupials) almost ubiquitously demonstrate unimodal richness patterns with the highest richness at intermediate elevations (robust, informative gradients (RIG) = 54; McCain, 2005). Bats demonstrate two global patterns: half of the studies found decreasing species richness with increasing elevation and the other half found unimodal richness patterns (RIG = 12; McCain, 2007). As stated above, Rahbek found that plants tend to show mostly unimodal richness patterns (RIG = 21; from Rahbek, 2005, fig. 3f). Birds show more variation in their elevational richness patterns: 30% are decreasing, 43% have high diversity across most of lower portion of the gradient then decrease (low plateau in diversity; e.g., Fig. 1a), and the final 27% have unimodal richness (RIG = 95; data assembled by C. M. McCain (CMM)). Analyses of global elevational gradients for amphibians, reptiles, and invertebrates also generally find robust support for these three main patterns: decreasing, low plateau, and unimodal.

Mountain regions often host a large fraction of endemic species (e.g., Orme *et al.*, 2005). Considering that isolation is an important factor for speciation it is no surprise that fraction of endemic species tend to increase with altitude resulting in a peak in species richness at intermediate elevations above the peak in total species richness. For vascular plants in the highest mountains of the world the fraction of endemics increases linearly from the lowlands to the highest point where plants are found (around 6000 m above sea level) (Vetaas and Grytnes, 2002). This results in a peak in endemic richness around 4000 m, whereas the total number of species peaks around 1500 m. Studies on avian mountain endemics demonstrated their greatest diversity at intermediate elevations between 1500 and 3000 m, although somewhat lower on shorter mountains, even though overall diversity decrease monotonically with elevation (e.g., Stotz *et al.*, 1996). Such contrasting patterns in total species richness and endemic species richness are most likely commonplace along elevational gradients, particularly for highly diverse groups.

IV. DISCUSSION OF POSSIBLE CAUSES

Elevational gradients are invaluable for discerning between diversity hypotheses. The small spatial scale, the thousands of independent replicates on mountains across the globe of various heights and in various climates, the high variability in richness patterns among taxonomic groups, and the predictable trends in abiotic factors with elevation allow globally distributed elevational gradients to be used as natural experiments, allowing for rigorous testing of hypotheses. The causes commonly mentioned for elevational patterns in species richness are very similar to the causes used to explain other broad-scale factors in species richness. These can be grouped into four categories: climatic hypotheses based on current abiotic conditions, spatial hypotheses of area and spatial constraint, historical hypotheses invoking processes occurring across evolutionary timescales, and biotic hypotheses (e.g., community overlap (ecotones), source–sink dynamics, and habitat heterogeneity). Below, we describe some of the most commonly asserted hypotheses and assess their current level of support.

A. Climatic Hypotheses

Climatic variables like temperature, rainfall, and productivity are probably the most commonly cited causes for broad-scale patterns in species richness and elevational patterns are no exception. Temperature has a simple relationship with altitude as it decreases monotonically by 0.3–0.6°C per 100 m elevational gain. Rainfall often follows a more complex relationship with altitude and maximum rainfall is often found at intermediate elevations, but is also known to increase with elevation or be high across a broad band of low-to-intermediate elevations. In tropical areas, the zone of maximum humidity often corresponds to the cloud zone and horizontal precipitation from low-lying clouds can significantly increase the water availability at those elevations.

Climate may affect elevational species-richness patterns in several ways. First, climatic tolerances of the studied species may put restrictions on how many species can survive at the different elevations. This will have different effects on different species groups. Some species groups (e.g., epiphytic plants and salamanders) are dependent on high and constant moisture, whereas others may be restricted by a certain winter temperature. As a result, different species groups will show different elevational richness patterns, exactly what was demonstrated by Whittaker's early studies and confirmed by McCain's meta-analyses. Second, species richness may depend on productivity through the number of individuals that are found in an area. Higher productivity leads to higher number of individuals, which in turn leads to higher species richness. Primary productivity is dependent on temperature and precipitation. Because rainfall in many cases increases with elevation or has a humped relationship with altitude, highest productivity may be found in the middle of the elevational gradient in many cases. In arid or seasonally dry areas where precipitation is low at the lowest elevations, productivity may decrease with temperature because higher temperature leads to higher evaporation. This may explain differences in patterns between mountains with wet versus dry local climates so that species richness on wet mountains is monotonically decreasing with increasing elevation, whereas on dry mountains richness peaks at mid-elevations (Fig. 1b). Evaluation of this model shows very good support for bats, as all bat diversity patterns studied from dry-based mountains show peaks in richness at intermediate elevation, whereas all but one study on wet-based mountains show strongly decreasing bat richness with increasing elevation (McCain, 2007). Brown and Lomolino (1998) also concluded that dry montane environments may show mid-elevational peaks in diversity across multiple taxonomic groups due to the higher water availability at intermediate elevations.

B. Spatial Hypotheses

1. Area

The classical species–area relationship is often asserted to explain elevational species-richness patterns, predicting more species in elevational bands that cover more area. Most area on mountains occurs at lower elevations (Körner, 2000) but in some areas, particularly mountainous regions, steep valleys at low elevations cover less area and lead up to a large plateau at intermediate elevations, and in such cases the area is more extensive at mid-elevations. This variation predicts different elevational richness patterns between mountains if area determines richness and may serve as an exceptional test system for evaluating the importance of area on broad-scale patterns.

So far, very few studies have investigated the effect of area on elevational patterns in species richness. McCain (in press) evaluated the species–area relationship across 34 globally distributed mountains. Area influences montane richness patterns to a surprisingly low degree; overall only 38% of the studies showed strong responses to area (i.e., had a significant impact on the elevational pattern in species richness). In these cases, correcting for area generally resulted in changing linearly decreasing patterns to mid-elevational richness peaks, but the area effect does not appear to be consistent enough among studies to be the main driver of richness patterns (McCain, in press).

2. Mid-Domain Effect (MDE)

The mid-domain effect (MDE) is a relatively new hypothesis for explaining broad-scale patterns in species diversity (reviewed in Colwell *et al.*, 2004). The hypothesis predicts a humped species richness pattern when species ranges are randomly distributed within a geometrically constrained domain (i.e., base and top of a mountain). A terrestrial species range cannot extend over the top of the mountain or below the base at sea level or the lowest regional elevation. Most of the elevational studies published lately discuss the potential of MDE as an explanatory factor. The conclusion from these results is that MDE predictions can sometimes be highly correlated with the observed pattern (e.g., Kluge *et al.*, 2006), but in the majority of the studies the fits to the model are low (mean $r^2 = 0.18$; McCain, 2005, 2007). MDE may play a role in concert with other factors such as area and climate, but are probably not the main driver of elevational richness patterns.

C. Biotic Hypotheses

1. Ecotone and Source–Sink

Along elevational gradients, the distance between very different climatic zones and hence also between different communities and biomes are short. This implies that there will be short distances between optimal and suboptimal areas for many species along the gradient. This may result in a net flow of seeds or propagules from optimal to suboptimal areas. Even though a population of a species usually would not survive in a suboptimal area over time the extra propagules received from populations in the nearby optimal areas (usually called source populations) may result in persistence of the populations in the suboptimal areas (sink populations) (Pulliam, 1988; mass effect is another term used to describe this process, Shmida and Wilson, 1985).

Source–sink dynamics will generally inflate species richness along the whole elevational gradient as new species are added locally by sink populations. This may affect elevational species-richness patterns in two ways. An elevational pattern in species richness may be created by source–sink dynamics only if some areas receive more sink species than other areas. This may be the case around ecotones where more sink species may be found than in surrounding areas resulting in peaked species richness around ecotones. Studies that have looked for the ecotones specifically have difficulties in actually detecting an abrupt change in species composition or increased species richness around the assumed ecotones (Terborgh, 1985; McCain, 2004; but see Grytnes, 2003 and Kessler, 2000), indicating that this may not be important for shaping the elevational richness pattern, but only very few studies have looked at this explicitly. Alternatively, source–sink dynamics may create an elevational pattern if the lower and upper part of the elevational gradient receives less sink species than the mid-elevational parts. Mid-elevational areas will receive sink populations from source populations both above and below, whereas the upper and lower part of the gradient will only receive sink species from one direction. This will create a humped pattern, with maximum species richness in the middle of the elevational gradient. It is, however, very difficult to evaluate this hypothesis rigorously because of problems in robustly defining sources and sinks.

2. Habitat Heterogeneity

Heterogeneity will certainly have a large effect on species diversity. It is however, difficult to say anything general about how heterogeneity will vary with elevation. The relevant type of heterogeneity will depend very much on the species group studied and on the scale of study. For bird species that forage in forest trees or for epiphytic plants the important heterogeneity will certainly depend on height of canopy and number of strata that can be defined in the forest (e.g., MacArthur and MacArthur, 1961; Terborgh, 1977). This will generally decrease with altitude, or be related to productivity. An opposite example can be found by looking at moisture variation at relatively small scale. At high elevations, water runs in small canals creating a high heterogeneity of moisture. At lower elevations, the water gathers in larger and larger waterways and at small to intermediate scales the moisture heterogeneity will increase with elevation. Owing to the difficulty in defining the taxon-appropriate habitat heterogeneity and obtaining robust field measurements, habitat heterogeneity has not been tested rigorously beyond the elevational studies of Terborgh (1977).

D. Historical Hypotheses

Ultimately, species-richness patterns result from differences in speciation, extinction, and immigration rates. Speciation rates, extinction rates, and clade age are thought to be correlated with latitude causing the highest richness near the equator through influence from climate and/or area (Brown and Lomolino, 1998; Rosenzweig, 1995). Examining elevational gradients eliminates this problem by examining diversity patterns within a single region of potentially uniform clade ages and latitudinally similar speciation and extinction rates. The predictions of evolutionary rates have been less developed along elevational gradients, but in addition to a positive relationship between climate and evolutionary rates that may cause high evolutionary rate at low elevation; the increasing isolation toward higher elevation will work in the opposite direction. Elevational trends in evolutionary rates will certainly have little effect on mountains whose biota are mainly comprised of organisms that have colonized from a larger regional pool (e.g., areas covered by ice during last ice age) compared with large mountain ranges like the Andes or Himalayas that also have endemic species generated through various gradients of speciation, extinction, and climatically fluctuating range shifts. The consistency of taxonomically and thus ecologically linked climate trends on elevational gradients (e.g., small mammals, bats, and birds; Fig. 1) lends support not only to current climate drivers but also to past climatic affinities. It may be that the signal of highest richness on mountains—in wet and warm conditions—is because these were the conditions under which most taxonomic groups and species originated. This lends support to the new ideas of niche conservatism (e.g., Wiens and Donoghue, 2004), which posits that modern large-scale species-richness patterns result from the fact that most modern groups and species originated when the majority of the Earth was experiencing tropical-like conditions and these strong affinities still exist in current climatic regimes.

V. CONCLUSIONS

The unique opportunities for evaluating hypotheses for broad-scale patterns along elevational gradients in species diversity have not been fully utilized to date. Comparing independent transects and searching for similarities and differences in patterns between transects and among taxonomic groups in different climates (tropics, deserts, and temperate regions), biogeographic regions (islands and continents) or between transects on mountains of different size or aspect (dry versus wet slopes) will certainly improve our understanding of mechanisms underlying broad-scale patterns in diversity. We need to develop more predictions specifically for comparisons of multiple elevational transects (as those shown in Fig. 1b), gather robust climatic data at small spatial scales, and optimally design new elevational studies to test predictions of diversity theory. Elevational trends in other aspects of species beyond diversity may help define other important aspects of global ecological patterns. For example, studies of elevational trends in range size coupled with physiological tolerances will improve our understanding of the role of climatic tolerances driving broad-scale diversity patterns (e.g., Janzen, 1967: why mountains are higher in the tropics) and the potential impacts of climate change. Similarly, understanding how biotic interactions (e.g., disease, food resources, and competition) influence species ranges and abundance patterns is fundamental to understanding niche dynamics as well as the strength of coupled responses to climate warming. For these reasons and because climatic shifts may be more rapid along the smaller-scaled montane gradients, elevational gradients may be ideal for long-term monitoring of species responses to climate change.

See Also the Following Articles

DIVERSITY, COMMUNITY/REGIONAL LEVEL • LATITUDE, COMMON TRENDS WITHIN • SCALE, CONCEPT AND EFFECTS OF • SPECIES–AREA RELATIONSHIPS • SPECIES DIVERSITY, OVERVIEW

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