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## Elevation gradients of species-density: historical and prospective views

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### ABSTRACT

Studies of elevation clines in diversity and composition of ecological communities date back to the origins of biogeography. A modern resurgence of interests in these elevational clines is likely to contribute important insights for developing a more general theory of species diversity. In order to gain a more comprehensive understanding of geographical clines in diversity, the research programme for montane biogeography should include statistically rigorous tests of apparent patterns, comparisons of patterns among regions and taxonomic or ecological groups of species, and analyses of clines in environmental variables concurrent with biogeographical surveys.

The conceptual framework for this research programme should be based on the assumption that elevational gradients in species diversity result from a combination of ecological and evolutionary processes, rather than the presumed independent effects of one overriding force. Given that montane ecosystems are hot spots of biological diversity, an expanded and integrated programme for biogeographical surveys in montane regions should provide valuable insights for conservation biologists.

**Key words** diversity theory, elevational gradients, montane biogeography, mountains, species-density, species richness.

### AN HISTORICAL PERSPECTIVE

The origins of biogeography are entwined with those of evolutionary biology — both fields being the natural, perhaps inevitable, products of the Age of Exploration, and both being punctuated by Charles Darwin's and Alfred Russel Wallace's seminal contributions during the nineteenth century. However, the origins of biogeography, the geography of nature, must reach far back in the early history of our species. As early humans moved across the primordial landscape, they must have been keenly aware of spatial variation in the natural world. Natural selection would ensure that these early hunters and gatherers learnt where best to hunt for particular types of game or search for edible and medicinal plants, and where to find shelters buffered from extremes of temperature, wind

and precipitation. Spatial variation in natural resources may have been a key impetus for dispersal, migration and colonization of early humans across the continents and to distant archipelagoes (see Howells, 1973; Clark, 1992; Flannery, 1994; Gamble, 1994). One can only guess that this variation seemed both obvious and predictable.

The principle of spatial autocorrelation, that environmental conditions vary in a non-random manner along geographical gradients and that more distant sites also tend to be more dissimilar, must have been familiar to these early hunters and gatherers. It is likely that they also realized that spatial variation in the environment is accentuated along key landforms, especially mountains. How could they not notice the striking transitions and turnover of elevational belts of habitats, from deserts or thick forests in the

lowlands to treeless tundra and ice fields at the summit — all of which could be seen from one vista or covered along an ascent of just a few hours.

This vital knowledge of biogeographical variation continued to accumulate throughout our development as a dominant species, particularly during the last few centuries when we expanded the scope of our understanding of the natural world from local and regional scales to what would eventually become a truly global understanding of the geography of nature. Biogeographers and evolutionary biologists of the sixteenth, seventeenth and eighteenth centuries, then called 'naturalists' and 'geologists', travelled to the distant and diverse corners of the terrestrial world, all with a common goal — to understand the origin, spread and diversification of nature. Many, if not most of them, saw this as a sacred quest to serve their God — the Creator of these natural wonders and their underlying principles (the 'laws' of nature).

What we now call elevational gradients in biotic communities were central to some of the most general theories of the origin of life. According to Linnaeus, early earth was covered with water, except for its highest mountain top (believed to be Mount Ararat), which was the site of Paradise and perhaps Noah's landing as well (Linnaeus, 1743). As was well known to Linnaeus and many of his contemporaries, along the slopes of this one mountain could be found a compressed and very orderly succession of climate, vegetative zones and animals — a series of biomes mimicking at a local scale that which stretches from the equator to the poles. According to Linnaeus, sea levels of the world's primeval ocean dropped as the waters penetrated into the porous earth, exposing more and more land, which was soon colonized by plants and animals that migrated down from their respective elevational zones along Mount Ararat.

Later, elevational gradients in biotic zones would also form the basis for Willdenow's (1805) theory of the origins and spread of life. Instead of just a single, montane origin, Willdenow hypothesized that within each geographical region of the globe, plants and animals were first placed, and later survived the Great Flood on the many mountain ranges that are broadly dispersed across the globe. Each of these had

their own biota which, even after spreading down the slopes and to the next geographical barrier, maintained some distinction from the biota of other regions.

Willdenow also made the key observation that geographical variation in plant communities was strongly tied to climate.

Soil, situation, cold, heat, drought, and great moisture are all of powerful influence on vegetation (Willdenow, 1805, p. 348).

Indeed, it is clear that Willdenow attributed both latitudinal and elevational gradients in species diversity to corresponding variation in heat. As Willdenow (1805, p. 349) put it,

... the warmer the climate, the greater must be the number of growing plants.

Thus, nearly two centuries ago we had a clear and accurate description of two principle patterns of modern biogeography (latitudinal and elevational gradients in diversity) and a unifying, albeit rudimentary, causal explanation for those patterns (in fact, one that seems to be an early articulation of the species-energy theory; Wright, 1983; Currie, 1991).

The elevational gradient continued to serve as a heuristic tool and natural experiment for generations of scientists: from von Humboldt's (1849) legion of detailed observations along Mount Chimborazo in the Ecuadorian Andes in the early 1800s, to those of Darwin (1839, 1859) in the Chilean Andes, Wallace in Indonesia (1876, 1878), Joseph Dalton Hooker, Asa Gray and C. Hart Merriam (1890) in the North American Rockies during the mid- and later decades of the 19th century, to Robert H. Whittaker's (1960; Whittaker & Niering, 1965) surveys in the Santa Catalina, Great Smokey and Siskiyou Mountains (southeastern and western North America) and James H. Brown's (1971a) research in the Great Basin of North America. In recent years, however, elevational gradients have received much less attention than what are viewed to be ecology's most general patterns — latitudinal gradients in diversity and the species-area relationship. This seems unfortunate and unproductive for a number of reasons. Elevational gradients, in addition to their distinguished historical position in the development of biogeography, ecology and evolutionary biology, may be equally as general and

may be intricately related to species–latitude and species–area relationships. Linnaeus (1743), Forster (1778), Willdenow (1805), von Humboldt (1849) and many of their contemporaries saw the elevational and latitudinal patterns as responses to the same environmental factors (namely, spatial clines in climate and energy). Perhaps just as obvious to these early scientists, area decreases with elevation. Thus, all the explanations for the species–area relationship may have been applied to elevational gradients in diversity as well; lower elevational zones (larger areas) having: (1) greater total amount (across their entire extent) of solar energy, resources and population numbers; (2) more refugia and more space for species with larger home ranges; (3) greater diversity of environments; and (4) greater potential for serving as a target for potential immigrants (Brown & Lomolino, 1998; but see below). In his seminal monograph on geographical ecology, Robert MacArthur (1972) clearly described montane ecosystems as simply special cases of the equilibrium/island paradigm. Because they are both small and isolated (from other montane ecosystems), montane communities should have relatively high extinction rates and low immigration rates. Therefore, their equilibrium species numbers should be lower than those of lowland communities (see also MacArthur & Wilson, 1967).

## A RESEARCH AGENDA FOR MOUNTAIN BIOGEOGRAPHY

We are now experiencing a resurgence in montane research, largely owing to the efforts of a growing number of scientists committed to addressing the Linnean shortfall (the great discrepancy between the number of identified and existing species) and to developing a more comprehensive understanding, and more effective strategies for conserving, biological diversity. The modern research programme in montane biogeography builds upon the classic studies of the past two centuries and, to a significant degree, may have been revitalized by James H. Brown's present studies of montane biogeography of Great Basin mammals (1971a, 1978).

The four contributions to this special feature (Heaney, 2001; Md. Nor, 2001; Rickart, 2001; Sánchez-Cordero, 2001) are among a number of distinguished studies that have been conducted

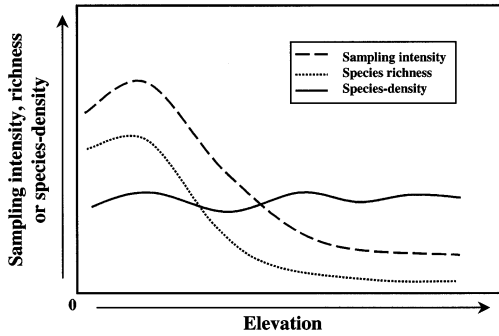
during this modern period of montane biogeography. In addition to other special features (e.g. that edited by John Haslett (1997) entitled 'Mountain ecology: organism responses to environmental change', *Global Ecology and Biogeography Letters*, Vol. 6), recent syntheses and general reviews have begun to re-evaluate the nature and generality of elevational gradients in diversity, and to clarify the conceptual framework and set the agenda for future research (Rahbek, 1995, 1997; Rosenzweig, 1995). In order to gain a more comprehensive understanding of patterns of diversity, in general, the research programme for montane biogeography should include the following.

**1** *Statistically rigorous tests of the nature of the pattern for particular taxa and mountain ranges.* Is the trend significant; if so, does diversity increase or decrease with elevation, or does diversity peak at an intermediate elevation?

**2** *Comparisons of elevational trends in diversity among taxa and among mountain ranges. Comparisons of elevational trends in distribution and abundance of particular species among mountain ranges.* The comparative approach has served biogeography well throughout its history and, given the typically unwieldy temporal and spatial scales of this field, may often be the only logistically feasible and ethically acceptable approach for studying such large-scale patterns in diversity.

**3** *Analyses of clines in environmental variables both within and among mountain ranges* — in particular, those directly associated with causal explanations for the predicted or observed patterns.

Essential to this research agenda is a more explicit consensus on the term 'diversity'. In the earliest articulation of elevational gradients, the term diversity referred to what we now call species-density, i.e. the number of species detected per area sampled, or per spatially standardized survey effort. Therefore, it seems that the best way to achieve the goals of the above research agenda is to conduct systematic surveys, using the same approach (same complement of detection techniques, spacing of survey sites and duration of surveys) across elevations, zonal habitats and mountain ranges. In order to achieve the ultimate goal of developing a more general, causal explanation for elevational patterns in species-density, surveys also should include standardized measurements of environmental variables concurrent with community surveys.



**Fig. 1** Variation in sampling intensity may generate spurious patterns in species richness along elevation gradients; i.e. variation in richness may simply reflect variation in sampling intensity along this elevational gradient. However, under the null hypothesis that these apparent patterns are artefacts and not the results of any underlying ecological or evolutionary processes, species-density (number of species detected per standardized survey effort) should not vary with elevation.

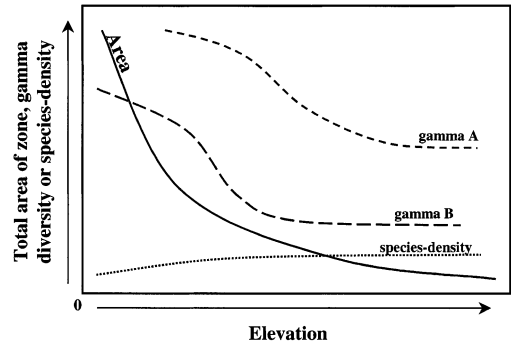
The following theoretical framework may prove of some value in designing and evaluating the results of these surveys and, ultimately, contributing to a general theory of species diversity.

### Sampling artefacts

The reported 'pattern' is actually a spurious outcome of biases in the sampling regime.

**Prediction:** *Species richness varies directly with the sampling intensity (measured as time or effort expended per site, transect or quadrat).*

Here the assumption is that while species richness may vary with elevation, species-density does not change significantly, or that it does not peak at an intermediate elevation. According to this null hypothesis, the apparent decline or peak in observed species richness is simply consistent with corresponding clines or peaks in sampling intensity (Fig. 1). Again, this is why it is important to focus on patterns in species-density (number of species per standardized survey), not an unstandardized measure of richness. As long as the biological surveys are conducted using a spatially and temporally standardized and systematic protocol, and it is not biased towards detecting



**Fig. 2** As we move up a mountain, the total area of each vegetation zone usually declines. As a result, gamma diversity (total number of species in a particular zone) should also decline, although the number of species detected within a standardized sample area (i.e. species-density) may not vary substantially with area of the zone. In fact, because the slope of the species–area relationship is steepest for the smallest ecosystems and area tends to decline with elevation, species-density of montane biotas may (all else being equal) actually increase with increasing elevation.

species restricted to any particular elevational zone (especially the lowlands or intermediate elevations) or habitat, this null hypothesis can be rejected.

### Biogeographical explanations

The many alternative explanations for elevational gradients in species-density are associated with four features of montane systems: elevational gradients in area; elevational gradients in climate; geographical isolation of montane communities; and feedback among zonal communities.

#### *Gradients of area*

Because area of zonal communities declines with elevation, all the causal explanations for the species–area relationship may have been applied to elevational gradients in diversity.

**Predictions:** *Gamma diversity (total richness of an entire elevational zone) should vary directly with total area of each elevational zone, peaking in those zones that cover the largest area. Within the same mountain range, different species groups should exhibit the same qualitative pattern of gamma diversity vs. area (Fig. 2).*

This area-based explanation seems reasonable at face value, but only when applied to patterns in gamma diversity, not to gradients in species-density. Just because a larger ecosystem has a greater amount and diversity of resources, habitats and refugia over its entire extent, it does not follow that each of its local sites must share these properties. On the other hand, high dispersal rates within relatively large ecosystems may enhance local diversity if transients from other sites within the same elevational zone supplement local communities. While this 'mass effect' (Shmida & Whittaker, 1981; Schmida & Wilson, 1985) may be significant in some situations, I suspect it is unlikely to account for very general patterns in species-density along elevational gradients. In fact, because the slope of the species-area relationship should be steepest for the smallest ecosystems and area tends to decline with elevation, species-density may (all else being equal) actually increase with increasing elevation (Fig. 2). Biodiversity surveys conducted in mountain ranges with extensive plateaus (i.e. high-elevation and large ecosystems) may, while an exception to the general relationship between area and elevation, prove to be especially instructive means of testing area-based predictions.

#### *Climatic gradients*

The many components of climate and local environment (including temperature, precipitation, seasonality, disturbance regimes and soil characteristics) vary in a non-random fashion along most elevational gradients.

*Predictions: Species-density should vary with local environmental and climatic conditions, and peak at elevations characterized by the combination of conditions documented (by independent means) to be optimal for the focal species. The relative position of elevational peaks in species-density should vary in a predictable manner among species groups that differ in environmental affinities and fundamental niches. Among mountain ranges, elevational peaks in species-density should also correspond with elevational shifts in climate and environmental conditions.*

The combined effects of spatial covariation among this suite of variables may cause productivity to peak, and environmental stress to

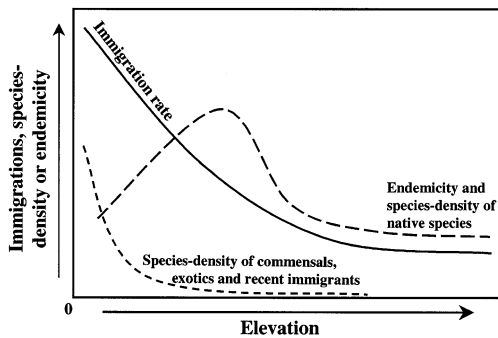
be minimal, either in the lowlands or at some intermediate elevation zone. Because the terms 'productivity' and 'environmental stress' are specific to the focal species group, optimal or peak conditions should also vary, but in a predictable fashion, from one species group to another. Equivalently, if this climate/niche-based hypothesis is valid, then the elevation of peaks in species-density should vary in a predictable fashion with elevational shifts in climatic and environmental gradients among mountain ranges. Thus, the Massenerhebung effect (the tendency for vegetation zones to occur at lower elevations on smaller mountains; Richards, 1952, pp. 346–368) and downward shifts in climatic regimes and zonal communities with increasing latitude, may serve as natural experiments to test this causal explanation for species-elevational gradients.

It is also important to note that extant patterns of diversity along elevational gradients may, to some degree, represent historical legacies of past climates. For example, diversity of some high elevational communities may have not yet recovered from the effects of alpine glaciers which extended downward during some previous glacial maximum.

*Isolation of montane communities: clines in immigration, extinction, speciation and anthropogenic disturbance.* The complexity of the natural world, and the models we create to explore it, derive not just from the number of environmental variables considered, but from patterns of covariation and potential interaction among those variables as well.

*Prediction: Immigration rates into each zonal community should decline with elevation, and species-density and endemism of native species should peak at intermediate to upper elevations (Fig. 3). Species-densities and population densities of commensals, taken separately, should decline with increasing elevation.*

In general, high elevation habitats are not just smaller, but they are also more isolated — isolated from other mountains, from other zonal communities within the same mountain, and from human populations. Thus, as we move up to higher elevations, immigration rates should decline and extinction rates of local populations should increase (because populations at high elevations



**Fig. 3** Because higher elevation communities are more isolated from other communities, immigration rates should decline with elevation. The influence of anthropogenic activities and commensal and exotic species, which tend to concentrate in lowland regions, should also decline with increasing elevation. On the other hand, speciation rates, along with endemicity and species-density of native species, should increase with elevation and perhaps peak at intermediate elevations (where the combination of area and isolation may be more optimal for persistence and divergence of native species).

are both smaller and less likely to be 'rescued' by individuals dispersing from other zones; the 'rescue effect' of Brown & Kodric-Brown, 1977; Lawton *et al.*, 1987). On the other hand, upper elevational zones may provide the geographical isolation required for speciation. If the montane zones are both isolated and large enough to allow population persistence and divergence over evolutionary time, they may represent hotspots of speciation and endemicity (Kikkawa & Williams, 1971; Terborgh, 1977; McCoy, 1990; Rahbek, 1995; Heaney, 2001). Finally, the intensity of human disturbance has an equally strong geographical signature: anthropogenic disturbance usually declines with increasing isolation. Consequently, populations of imperilled species tend to persist in the most isolated regions of their historic range: on an island, along the range periphery, or at the higher elevations of their historic range (see Lomolino & Channell, 1995, 1998; Channell, 1998; Channell & Lomolino, 2000a, 2000b).

The combined effect of these processes with opposite patterns of spatial variation (i.e. some increasing while others decreasing with elevation) should usually be a peak in species-density at an intermediate elevation.

#### *Feedback among zonal communities*

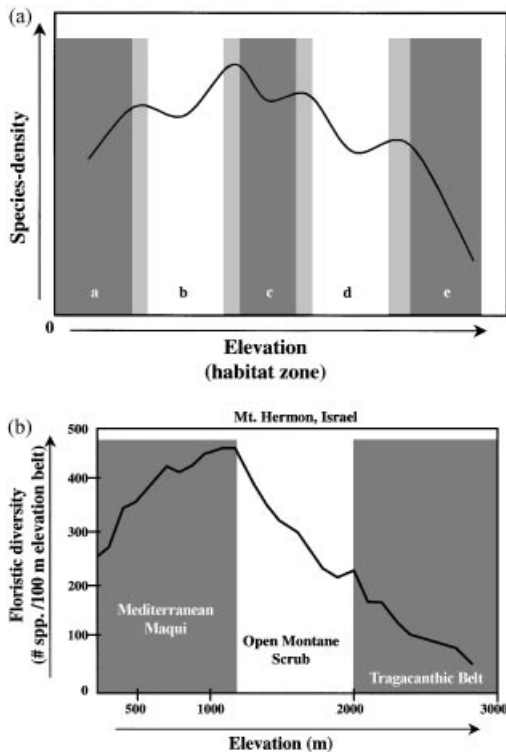
Part of the elevational pattern, namely peaks in species-density at intermediate elevations, may result from, or be accentuated by, interactions and feedback among zonal communities.

**Predictions:** *Species-density should peak at an intermediate elevation and the peak should occur at a transition zone between the two species-rich, juxtaposed communities. In addition to this major peak, species-density should exhibit repeated minor peaks at transitions between other zonal communities (Fig. 4).*

Biotic exchange among zonal communities will most likely create a peak in species-density along a transition zone between two rich and distinct communities, rather than deep in the interior of either community. This is simply an elevational equivalent of the well-known ecotone effect, which may also be associated with rescue and mass effects (Brown & Kodric-Brown, 1977; Shmida & Wilson, 1985; Stevens, 1992).

Yet biotic exchange, and therefore the species-density of transition zones, is not likely to be uniform across the entire elevational gradient. First, the magnitude of the exchange among biotas and that of the ecotone effect as well, is directly dependent on the richness of the juxtaposed communities. Secondly, elevational gradients are always truncated, with the height of the summit setting an absolute limit to the number of communities comprising the gradient (see Rahbek, 1997). At the lower elevations of montane surveys, substantial mixing and range overlap can occur from both directions (above and below); but as elevation increases, the potential contribution from higher zonal communities must decrease. Thus, as we move along elevational gradients we expect repeated, minor peaks in diversity corresponding to transition zones among elevational communities, but the absolute diversity of these transition zones should decline with elevation, at least for the higher zones. Note, however, that the above prediction is based on the assumption that elevational zones form integrated units which are marked by distinctive transition zones.

Finally, biological surveys along elevational gradients also have what can be termed a 'soft truncation', one set by the researchers. Few, including the most dedicated and well-funded



**Fig. 4** (a) Biotic interchange may create a series of repeated, minor peaks in species-density at transition zones between zonal communities, with a maximum peak located at the transition zone between two species rich communities. In this hypothetical example, zonal communities are labelled a–e and illustrated by alternating bands of dark grey and white (transition zones in light grey). (b) Floristic richness (number of species in each 100-m elevation belt) along the slopes of Mt Hermon, in the Middle East (redrawn from Shmida & Wilson, 1985, Fig. 11) exhibit the predicted pattern of repeated peaks in species-density within transition zones.

scientists, extend their elevational surveys from summit to sea level. While this is both practical and entirely justified, it is important to question whether species-density may have peaked at some lower, 'intermediate' elevation (i.e. between the actual lowlands and the lower limits of the study; see Fig. 3). It is just as important to verify that the survey protocol was not unintentionally biased to detect species of a particular elevational zone.

## DISCUSSION

As a growing number of ecologists and biogeographers have recently argued (e.g. Ricklefs & Schluter, 1993; Lawton, 1996; Brown & Lomolino, 1998), general patterns in nature may result from the combined effects of many redundant, or convergent processes, rather than the presumed independent effects of one overriding force. A unified theory of species diversity may still be attainable, but is likely to be couched in the framework of some very fundamental principals of physics — such as self-similarity and scaling relationships — which impose similar constraints on a large number of geographical and biological properties. Clines in diversity along gradients of elevation, latitude, area and isolation may all owe their generality to nonrandom variation in factors that comprise the geographical template (*sensu* Brown & Lomolino, 1998). As we move up a mountain, these factors, along with associated biogeographical processes (immigration, extinction and speciation), vary in a predictable manner. Whether the diversity–elevational gradient is clinal, increasing or decreasing, or modal with a peak at intermediate elevations, will depend largely on patterns of covariation and interaction among these geographically explicit variables.

The contributions to this special feature represent exemplary studies of the nature and causation of the species–elevational gradient. Each of them focuses on similar groups of species (small mammals), but different mountain ranges and biogeographical regions. Three are based primarily on standardized field studies (Heaney, 2001; Md. Nor, 2001; Sánchez-Cordero, 2001). Each of these studies combines graphical and statistical approaches to analyse trends in species-density with elevation. While it may be premature to make statistically rigorous comparisons in species–elevational patterns among these studies, Rickart (2000) provides an interesting comparison of patterns for Philippine and Great Basin mammals, based on his extensive experience in both systems. Moreover, three of these studies (Heaney, 2001; Rickart, 2001; Sánchez-Cordero, 2001) compared species–elevational patterns among ranges within the same region (the two former studies using standardized survey protocols across their study sites). In addition, two of these studies compare patterns across taxonomically



and ecologically distinct groups of species (arboreal vs. terrestrial species — Md. Nor, 2001; bats vs. non-volant mammals — Sánchez-Cordero, 2001). Nor's study also includes cluster analyses of species distributions, which provided an objective assessment of the differences and potential biotic exchange among zonal communities. Heaney (2001), Md. Nor (2001) and, in particular, Rickart (2001), further dissect the diversity–elevational gradient by analysing patterns in elevational distributions of each species. Finally, they compare the clines and peaks in species-density to the locations of zonal habitats and the transition zones between those habitats.

The results of these studies, conducted on taxonomically related but ecologically diverse species and in widely separated geographical regions, reveal similar patterns in community structure across elevation. They all report hump-shaped patterns; i.e. diversity peaks at intermediate elevations (see also Gentry & Dodson, 1987; Rosenzweig & Abramsky, 1993; Colwell & Hurtt, 1994; Rosenzweig, 1995; Rahbek, 1995, 1997). The locations of the peaks, while varying substantially among mountain ranges, appear to correspond closely with transition zones between principal, zonal habitats and are therefore consistent with predicted patterns resulting from climatic gradients and biotic feedback among adjacent communities (e.g. overlap of geographical ranges within ecotones). Shmida & Wilson (1985) report a similar pattern for elevational gradients in plants (Fig. 4b).

Because detailed information on climatic gradients, dispersal, population persistence and anthropogenic disturbance are generally unavailable, it is difficult to evaluate critically some of the predictions associated with causal explanations for peaks in diversity at intermediate elevations. Yet it is clear from Nor's (2001) study that intermediate peaks in mammal and plant species correspond with peaks in precipitation and humidity, and with transitions between lowland and montane zones. It is also clear from Heaney's studies (2001) and those of others (Kikkawa & Williams, 1971; Terborgh, 1977; Gentry & Dodson, 1987; McCoy, 1990; Rahbek, 1995) that speciation and endemism peak at intermediate to high elevations. Biotic feedback, in this case interactions among species, appears

to influence strongly elevational distributions of small mammals. Heaney (2001) and Rickart (2001) report substantial elevational shifts and contractions of particular species of small mammals in response to the presence of other species (presumably, competitors: see Hall, 1946; Durrant, 1952; Findley, 1969; Brown, 1971b; Diamond, 1973, 1975; Noon, 1981; Lawlor, 1998). In addition, as Heaney (2001) and others have shown, elevational/niche shifts may be triggered by a variety of species, including those belonging to distantly related taxa — e.g. earthworms and ants (see also Heaney & Rickart, 1990; Olmstead & Wood, 1990; Rickart *et al.*, 1991).

## CONCLUSION

Taken together, the studies in this special feature present a picture that seems consistent with an emerging body of empirical patterns and general theories of species diversity. As we move across the geographical template, in this case along gradients of elevation, diversity peaks at an intermediate level along the cline. This level corresponds to the point where particular environmental factors may, taken separately, be less than optimal, but where the combined effects of these factors and associated processes and interactions promote co-occurrence of many species. For some taxonomic or ecological groups, the 'optimal elevation' may fall below the elevational range sampled and, thus, species-density will appear to decline with increasing elevation of sites surveyed. Given a much broader perspective on elevational gradients (one that includes the full range in elevation of a particular region), intermediate peaks in species-density may be a common, and perhaps the general pattern.

We must, however, continue to evaluate critically the generality of this emerging pattern and rigorously evaluate its multi-factorial, causal explanation. There are a number of notable exceptions to the reported hump-shaped pattern, even for very similar groups of mammals (e.g. Patterson *et al.*, 1989, 1996, 1998; Graham, 1990; see also Sfenthourakis, 1992). Rather than being discounted as noise around some more general, biogeographical pattern, we should realize that such exceptional cases may well prove invaluable in our attempts to develop a

more general theory of species diversity. It is just as important that we remain vigilant of sampling biases, which, in some cases, may create spurious patterns or inhibit our ability to detect authentic patterns of diversity along elevational gradients. For example, elevational trends in diversity of Peruvian birds appeared to be monotonic until Terborgh (1977, 1985) took into account the uneven sampling effort (which was lowest at mid-elevations), revealing a hump-shaped (intermediate peak) pattern in diversity (see Stotz *et al.*, 1996). The tendency to sample unevenly among elevational ranges is almost certainly not unique to this study. Again, in order to meet the challenge of a more general theory of species diversity, we should standardize and intensify our survey efforts across a greater range and higher resolution of elevations, and across a broader diversity of species groups and mountain ranges.

In addition to its heuristic value, an expanded and integrated programme for biogeographical surveys in montane regions will provide valuable insights for conservation biologists. Since the time of Willdenow and colleagues, montane systems across the globe were recognized as biodiversity hotspots — harbouring rich biotas, often with a highly disproportionate number of endemic species.

We find that mountainous countries are richer in plants than flat countries, and that in primitive mountains the number of plants exceeds that of the floetz [flat, like ice-sheets] *mountains* (Willdenow, 1805, p. 353).

Like the mythical biblical Flood that destroyed lowland plants and animals, today's burgeoning human populations now dominate lowland regions across most of the earth's surface. Mountains have become the last refugia for a great, albeit largely undetermined, number of threatened and endangered species. Thus, it is both timely and essential that biogeographers, ecologists and evolutionary biologists once again take up the challenge of describing and understanding patterns of biological diversity of mountain ecosystems.

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