

The elevational gradient of species richness: a uniform pattern?

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The decline in species richness with increasing elevation is widely accepted as a general pattern (Table 1). In as much as the elevational gradient is often claimed to mirror the latitudinal gradient, species richness is assumed to decrease monotonically (i.e. because of reduced temperature and consequent decrease in productivity). Perhaps because such a relation is intuitive, biologists have readily generalized the results of a few early studies of tropical birds as supporting a general biogeographic

Table 1 Typical examples of statements about the relationship between species richness and elevation from books and papers in major journals

"For all of these reasons, we expect the number of species to decrease with altitude and, in fact, it does" (MacArthur 1972, p. 107)

"In terrestrial habitats, variation in species diversity along gradients of elevation and available soil moisture are [sic] almost as general and striking as latitudinal variation" (Brown and Gibson 1983, p. 502)

"In terrestrial environments, a decrease in species with altitude is a phenomenon almost as widespread as a decrease with latitude" (Begon et al. 1990, p. 805)

"Just as change of physical conditions with altitude resembles in many respects the variation with latitude, so the decreasing diversity of most organisms with increasing elevation mirrors in most respects the latitudinal gradient of species richness" (Brown 1988, p. 62)

"biologists have long recognized that elevational and latitudinal species-richness gradients mirror each other" (Stevens 1992, p. 899)

"In terrestrial ecosystems, diversity generally decreases with increasing altitude. There appear to be no substantiating data for [the] 'mid-altitudinal bulge' as a general phenomenon" (World Conservation Monitoring Centre 1992, pp. 43,45)

"Decrease in the number of species with decreasing temperatures at higher altitudes is as conspicuous as the decrease with latitude (e.g. Brown and Gibson 1983), although exceptions occur" (Rohde 1992, p. 522)

pattern. This has resulted in "citation inbreeding". Here, I outline the supporting evidence for the generalization and discuss the influence of sampling regime and the often ignored influence of area. I then present a quantitative review of the data already present, although often ignored, in the literature. Altogether 97 papers (with 163 examples) have been reviewed. The analysis of these empirical data support the view that species richness declines with elevation, but not the view that this decline is necessarily monotonic. Some possible reasons for variation in the exact shape of the relationship between species richness and elevation for different taxa and zoogeographic areas are commented, but our understanding of the relation between elevation and species richness still appears to be immature.

The empirical basis for the "general pattern"

The generalization (Table 1) grew mainly from two studies dealing with tropical birds: one from the Peruvian Andes (Terborgh 1977), and the other from New Guinea (Kikkawa and Williams 1971). The textbook example from New Guinea was published as a short note based on compilation of the published distributional data (Kikkawa and Williams 1971). It was conducted at a time when the knowledge of the elevational distribution of New Guinean birds was still somewhat rudimentary. Another more detailed study on birds of New Guinea has also been cited as proof of the general pattern (Diamond 1972, cited in MacArthur 1972). However, Diamond's New Guinea data actually show a small peak in species richness at 1100 m with a marked decline in species richness only above this level.

The second textbook example was based on a carefully conducted field survey and critical data analysis (Terborgh 1977). Based on mist-netting and opportunistic

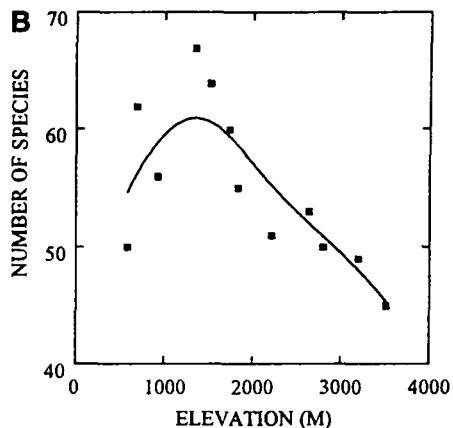
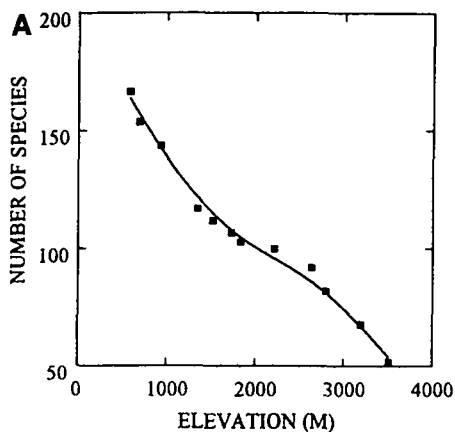


Fig 1 Species richness of syntopic birds versus elevation on an Amazonian slope of the Andes in Peru. Figure 1A is based on data not standardized for area and sampling effort, whereas Fig 1B is based on standardized samples of 300 mist-netted birds (data from Terborgh 1977). I have fitted the lines by distance-weighted least-squares smoothing.

field observations at camps situated along an elevational gradient on the humid east slope of the Peruvian Andes, Terborgh showed that species richness declined monotonically with elevation if the number of species is simply plotted against elevation (Fig 1A). However, when Terborgh tried to eliminate the effect of sampling time by standardizing his mist-netting data, a different pattern emerged (Fig 1B). Terborgh explained the emerging "hump-shaped" curve, which had a peak in species richness around 1400 m, as the result of a local "hot-spot" in resources (Terborgh 1977). Although this unexpected pattern is addressed through most of his discussion, only the first non-standardized graph is usually cited in the literature (e.g. Brown 1988). Though the use of under-

storey mist-netting data limited the scope of this study, it serves to demonstrate the strong effect that sampling effort can exert – especially in species-rich tropical forest where most species occur at low densities.

The importance of area

The effect of area on the relationship between species richness and elevation has rarely been considered, although we would expect area to have a significant impact on the form of the elevational pattern, as the relationship between area and species richness seems as universal as

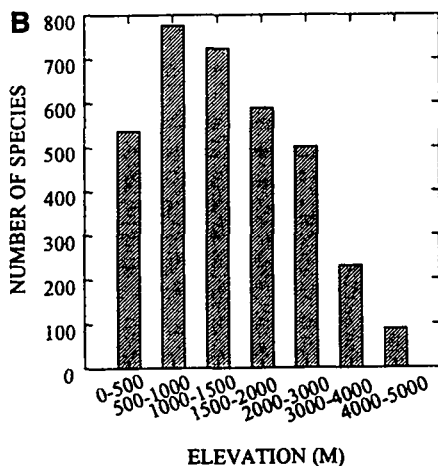
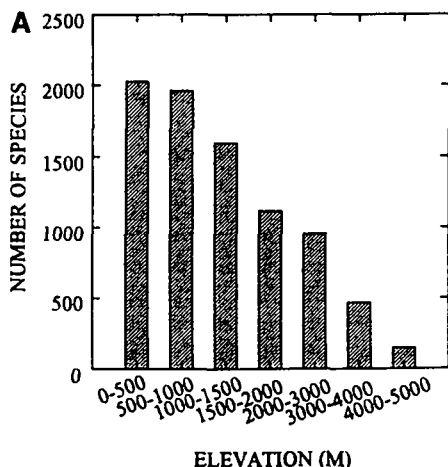


Fig 2 Species richness of South American tropical landbirds versus elevation. Figure 2A is based on data not standardized for area, whereas Fig 2B is based on data standardized for area set to 50 000 km² using equations for species-area curves ($\log S/\log A$ transformation) of each elevational zone (based on data from Rahbek unpubl.). Area is set to 50 000 km² because it is within the range of the original data upon which the equations are based, and is a size within the geographical regional scale (e.g. Wiens 1981, Rosenzweig and Abramsky 1993).

Table 2 Number of data sets ($n = 163$) found in the literature with data on the variation of species richness with elevation summarized by biomes (NT = non-tropical biomes, T = tropical biomes) and scale (R = regional, L = local), listed for studies conducted on mainland and island, respectively, and subdivided for whether the researcher(s) have attempted to standardize for the effect of area and sampling regime and/or effort, only one of these factors, or none ("non-standardized")

	Invertebrates		Vertebrates		Plants		Totals	
	NT (R/L)	T (R/L)	NT (R/L)	T (R/L)	NT (R/L)	T (R/L)	NT (R/L)	T (R/L)
Mainland								
Area and sampling	0/2	0/0	0/6	0/1	0/10	0/6	0/18	0/7
Area	0/0	0/0	0/0	1/0	0/0	4/3	0/0	5/3
Sampling	4/1	3/4	0/6	3/1	0/1	0/0	4/8	6/5
Non-standardized	9/11	4/6	3/0	17/4	1/0	8/3	13/11	29/13
Island								
Area and sampling	1/0	3/2	0/0	0/0	0/4	0/0	1/4	3/2
Area	0/0	1/0	0/0	0/3	0/0	0/0	0/0	1/3
Sampling	0/0	0/5	0/0	0/1	0/0	0/0	0/0	0/6
Non-standardized	0/5	2/5	0/0	5/2	0/0	2/0	0/5	9/7
Total	14/19	13/22	3/12	26/12	1/15	14/12	18/46	53/46

the latitudinal gradient. To understand the relationship between area and species richness along elevational gradients, especially on a regional scale, the effect of area must be considered since areas of equal-sized elevational belts may vary with elevation. Thus, areas often decrease with elevation because of generally steeper terrain toward the highest peaks. When landbird data from tropical South America, compiled at a regional scale using countries as units, are standardized for area, the relationship between species richness and elevation gives a hump-shaped curve (Fig. 2). However, area alone is unlikely to explain any global pattern of species richness, as close couplings can be expected to exist between biological diversification and habitat complexity (see also Rosenzweig 1992).

A quantitative review of the literature

The repeated citation of the same few studies provides a false picture of the amount and diversity of data published on the issue. I have been able to find the surprisingly high number of 97 papers, with 163 examples that give data on the variation in number of species with elevation. It is highly probable that additional data exist, as many data sets are published in little known journals, or in the "gray" literature.

Table 2 summarizes some characteristics of each data set (taxonomic group, region, scale and data treatment). The influences of sampling regime/effort and the effect of area are among the most influential biasing factors in most field studies of species-richness patterns, and, unfortunately, equally difficult to eliminate successfully. I have thus only judged whether an attempt was made to deal with these two factors, either in the design of the survey or afterward, during the data analyses. Remarkably, many of the papers reviewed do not give any details

on this subject. These data sets are classified as "Non-standardized" together with those with no attempt to standardize data (Table 2).

Unlike the traditional historical trend within most fields of biological research, most data sets are from the tropics (99 out of 163). The focus on the tropics is presumably related to the circumstance that tropical elevational gradients comprise a wider range of climatic variation than temperate elevational gradients. Out of 163 data sets, 68 are on invertebrates, 53 on vertebrates (including 36 on birds), and 42 on plants. The majority of the data sets comes from mainland biota (122), whereas 41 data sets are from islands.

As shown, standardizing for sampling effort or effect of area can have a significant influence on the emerging shape of the relationship between species richness and elevation. In 87 of the 163 data sets, the data have not been standardized for area or sampling effort (corresponding figures for tropical and non-tropical biomes are 59% and 45%). Only in 35 (21%) cases has a standardization been attempted for area as well as sampling effort (figures for tropical and non-tropical biomes are 12% and 36%, respectively).

Considering the high mobility of birds compared to other groups, the reliance by most reviewers on primarily bird examples to illustrate a universal relationship seems ill-founded, especially when the bulk of data in the literature actually derives from invertebrates and plants. Table 2 also provides an overview for which combinations of, for example, taxonomic groups, scale, and region we lack studies – especially those that consider the effect of area and sampling regime on data.

Methodological problems and patterns

In many studies, a stated decline in species richness with

Table 3 The relationship between species richness and elevation summarized by type of pattern. Only the 90 data sets (of 163) that provide data points spanning from below 500 m to above 1500 m are included (see text). The classification of each pattern is based on a visual examination of bivariate plots. NT = non-tropical biomes and T = tropical biomes.

Scale	Monotonically decreasing		Horizontal, then decreasing		Hump-shaped		Increasing		Other	
	NT	T	NT	T	NT	T	NT	T	NT	T
Regional										
Invertebrates		1	1	2	4	7				
Vertebrates		6		4		6				1
Plants		2			1	10				1
Total regional	0	9	1	6	5	23	0	0	0	2
Local										
Invertebrates	1	2	2	5		10	1			1
Vertebrates		3	1	3		2				
Plants		4	3	1	3	1			0	1
Total local	1	9	6	9	3	13	1	0	0	2
Total	1	18	7	15	8	36	1	0	0	4

elevation was restricted to only a part of the elevational gradient. In other cases, mid-elevational data were lacking. Others used correlation tests on data sets that include few stations from low- and mid-elevation, but many from higher elevations, thereby biasing their findings toward a strong negative correlation. In such instances, the data are inapplicable to support a monotonic relationship. Conclusions based on correlation tests sometimes ignore that stations at mid-elevation actually have more species than stations at low elevation.

To analyze the general variation of species richness with elevation, a minimum requirement for any data set is that it includes data spanning the entire gradient, albeit it becomes increasingly difficult to find appropriate gradients with continuous natural habitat along the entire gradient. This is especially a problem with respect to lowland stations, as lowlands and foothills often are the most disturbed elevational zone(s). Of the 163 data sets, 47 do not include data from below 500 m. In the descriptive analysis of the elevational pattern of species richness, I have only included data sets which are based on a gradient from below 500 m to above 1500 m (see Table 3). This limits the analysis to 90 data sets of the original 163: 37 on invertebrates, 26 on vertebrates (including 19 on birds), and 27 on plants. As for the entire data set, this subsample of data sets is biased toward the tropics with 73 data sets compared to only 17 from non-tropical biomes. It also has more data sets from mainland ($n = 71$) than islands ($n = 19$). Non-standardized data sets are dominant ($n = 49$). In only 13 data sets (14%) have attempts been made to take the effect of area and sampling into account. The corresponding figure for tropical data sets, which have been the main source of generalizations on the elevational gradient, is only 7% (5 of 73 tropical data sets), in contrast to 47% of the non-tropical data sets.

To conduct proper descriptive statistical analyses of the variation of species richness with elevation, the stations (i.e. the data points) must be reasonably equally distributed over the gradient, and the number of data points sufficient to reflect any marked changes in habitats/biomes over the analyzed gradient. Unfortunately these two requirements for an optimal data set are rarely fulfilled. As it is difficult to judge especially the latter criterion for most of the published data no attempt has been made to select or exclude data on this basis.

Comparisons of elevational patterns between taxa, latitudinal climatic zones, biogeographic regions or mainland versus islands could be misleading without correction for the area effect and differences in sampling regime. Comparisons of studies are also biased by differences in the species included, and sometimes further by limitations to specific trophic levels, guilds or habitat. These problems and the pronounced heterogeneity of the quality of data sets make it difficult to conduct proper critical statistical tests for each data set of the relationship between species richness and elevation that are mutually comparable. Still, disregarding these biases, a rough comparison based on a classification of the pattern in each data set by visual examination of bivariate plots serves to illustrate how ambiguous the pattern is, both within region, spatial scale and crude taxonomic groupings (Table 3).

A decline in species richness with elevation seems to be a general trend. Yet, a pattern where the species-richness curve is almost horizontal up to a certain elevation before declining, or is hump-shaped, seems more typical than a monotonic decline (Table 3).

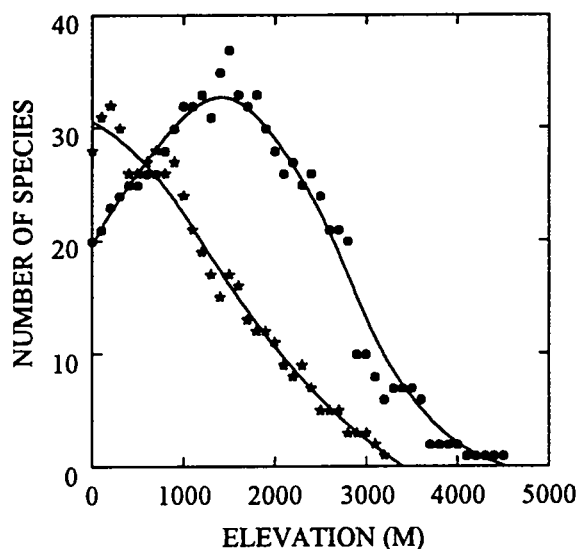


Fig 3 Patterns of species richness versus elevation may vary within the same area for different taxa, here illustrated by New Guinean bats (*) and rodents (●) (data compiled from Flannery [1990]) Data are not standardized for area and sampling effort Lines are fitted by distance-weighted least-squares smoothing

Just a reflection of the latitudinal gradient?

The decrease in species richness from the equator toward the poles is one of the most universal biogeographic patterns. This pattern has been shown across an array of taxa in aquatic as well as terrestrial ecosystems. Exceptions are few, and typically restricted to taxa with relatively few species (Rohde 1992). At first glance, the elevational gradient appears to share many climatic characteristics with the latitudinal gradient. Thus, Stevens (1992) claimed that ecologically restrictive climatic conditions appear to increase with elevation as they do with latitude. Furthermore, the harsh climate and relatively low species richness at the equatorial treeline seem to resemble the corresponding conditions found at northern and southern temperate latitudinal zones. The apparent resemblance of climate at high elevations and extreme latitudes makes it intuitively tempting to expect the elevational gradient of species richness to be just a mirror of that of the latitudinal gradient. The impression of a mirrored relationship is also indirectly imposed upon us by terminology traditionally used, as we often divide tropical mountains into tropical, subtropical, temperate and arctic (or alpine) zones (e.g. Chapman 1917). Yet, detailed analyses and comparisons of variation in biologically significant climatic parameters between the latitudinal and elevational gradient will reveal several important differences. For example, an important feature of climatic variation on the latitudinal gradient is the increased seasonality towards the poles. In contrast to this, mean tem-

perature remains fairly constant year round within the same bands on a tropical elevational gradient, and variation in temperature regime seems primarily to be diurnal. Interestingly, both types of variation in temperature regime are represented on temperate elevational gradients. One would expect this dissimilarity to have different impact on population maintenance processes on the two gradients and speciation.

Actually, the existence of a "plateau" or a "hump" on a curve comparing species richness with elevation should not be regarded as unexpected considering that – although temperature declines with elevation, another life-support factor, stable water supply, increases (at least to a certain elevation). Most elevational gradients have a more or less stable condensation zone (cloud zone) at a certain level, especially conspicuous in the tropics, causing favorable conditions for certain taxa (e.g. epiphytes at mid-elevation, which in turn create microhabitats and food for other taxa). As local climate can vary prominently over a few kilometers or hundred meters (e.g. between opposite slopes of the same mountain) in the tropics, the exact location of such a "climatic optimum" can vary considerably regionally and locally, causing differences in the shape of the elevational gradient even within the same taxa. The latitudinal gradient does not have such a "humidity peak". One could also add that habitat fragmentation necessarily increases with elevation but not necessarily with latitude.

Altogether, there seem to be no *a priori* reasons to believe that, climatically, the elevational gradient simply mirrors the latitudinal gradient.

A negative correlation between species richness and elevation fits well with the general acceptance that the lowland tropical rain forest has the richest biota on Earth (e.g. MacArthur 1972, Erwin 1988). Recent research has shown that this may not always be true on a regional scale (South American mammals [Mares 1992], and birds [Rahbek unpubl.]). Historically, a monotonic decline in species richness with elevation corresponds well with the many theories suggesting mechanisms by which increased energy availability often results in proliferation of different species rather than larger populations of existing species (e.g. Hutchinson 1959, Preston 1962, MacArthur 1972, Brown and Gibson 1983, Wright 1983). We now know that such an increase in species richness with productivity is not universal (e.g. Rosenzweig 1971, Carson and Barrett 1988). In fact, it has recently been suggested that the relationship is hump-shaped (Rosenzweig 1992, Rosenzweig and Abramsky 1993).

Final remarks

Understanding elevational patterns must be based on well collected qualitative data, and explanations must primarily be based on unravelling primary mechanisms, such as

physical causes, including climatic factors, the narrow width of the elevational gradient, and historical perturbations that shape the available species pool. Biotic interactions are secondary mechanisms that can be reflected in the emergent patterns. The variation of species richness with elevation might be connected to the reduction of temperature with elevation and the assumed corresponding reduction in productivity. However, other factors such as variation in steepness, geological perturbations, alterations of precipitation patterns, etc. might also be involved, probably with varying impact from case to case. For any correlation of species richness with variables measured over an elevational gradient, we need to examine whether the correlation reflects a direct coupling, or if it could be a result of interactions of several other factors.

The observation that high elevation supports fewer species than low elevation, which indirectly acted as a catalyst for the belief in a general monotonic decline, seems to be a general pattern (Table 3). Still, the pattern of species richness at low- and mid-elevations may differ between taxa as well as within taxa between different regions, and within the same region, at least on a regional scale (see example in Fig. 3). It is important to discriminate between patterns reflecting recent diversification and those reflecting long-term accumulation of species (Fjelds  1994). The latter could well be an equilibrium, provided that we compare areas that not only have similar average conditions but also resemble each other in habitat mosaic and dynamism. This could be a reason why the position of humps or bend of curves varies between different sets of data. Various taxa are also differently affected by abiotic factors, such as, for example, humidity.

Further studies, including analyses of primary-level processes that could influence the pattern, are needed to reveal whether general patterns exist within biogeographic regions, taxa, spatial scale, mainland versus islands, etc., or various combinations of these. Appropriate null-models should be considered before explaining elevational gradient patterns as results of climatic, biological and historical processes (Colwell and Hurtt 1994). Although a difficult task, the development of testable hypotheses is important to achieve significant progress within this field and to contribute to our general understanding of diversity patterns. This would be preferable to founding new generalizations on simple accumulations of case studies. Much is still to be learned about this topic, for now, we have to accept the unsatisfactory realization that we do not know whether a general relationship exists between species richness and elevation, or whether an universal explanation or model can be given.

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The complete list of papers which this Forum contribution is based on is available from the author.

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