

THE RELATIONSHIP AMONG AREA, ELEVATION, AND REGIONAL SPECIES RICHNESS IN NEOTROPICAL BIRDS

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Abstract.—The elevational gradient of species richness is often claimed to mirror the latitudinal gradient and has traditionally been explained by assuming a decrease in productivity with elevation and more recently by Rapoport's rule. The influence of area on the pattern has rarely been considered. Analyses of all South American tropical land birds (more than one-fourth of the extant bird species on Earth) are used to examine four species richness/elevation models: null model, Rapoport's rule, and monotonic or hump-shaped productivity/species richness relationships. To quantify the area effect, species-area curves were created for seven elevational zones. Not accounting for area, species richness declined monotonically with elevation, but area accounted for 67%–91% of the variation in species richness per zone. When area was factored out, a hump-shaped pattern emerged, with more species in the 500–1,000-m ($P < .005$) and 1,000–1,500-m zones ($P < .10$) than in the 0–500-m zone. Rapoport's rule and the monotonic productivity/species richness relationship were thus not supported. Instead, elevational turnover rates and numbers of shared species between zones suggested that the hump-shaped pattern reflects geometric constraints (as predicted by the null model) imposed by the narrow span of the gradient, and it is suggested that midelevational zones may represent sink habitats.

The distribution of organisms is not random. Yet, only a few patterns of species richness have been documented to be universal across time, geographical scale, and taxa. This is not unexpected, considering the complex interaction among ecological, historical, and evolutionary processes. Of the species-richness patterns reviewed by Brown and Gibson (1983), Brown (1988), and Begon et al. (1990), the species-area relationship (reviewed in Connor and McCoy 1979; Coleman et al. 1982; McGuinness 1984; Williamson 1988) and the latitudinal gradient (reviewed in Pianka 1966; Schall and Pianka 1978; Rohde 1992) are considered to be the best documented but also among the most debated. Recently, however, it has been argued that the latitudinal species-richness gradient is reasonably well understood (Rosenzweig 1992, 1995). Following McIntosh (1967), in this article I use the term *species richness* rather than *diversity* for the number of species (see also Peet 1974 for a review).

Other species-richness patterns, such as those occurring along elevational gradients, are poorly known. Nevertheless, an inverse relationship between species richness and elevation is believed by some to be just as general as the latitudinal gradient (e.g., MacArthur 1972; Simpson 1983; Brown 1988; Begon et al. 1990;

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Rohde 1992; Stevens 1992). This view has arisen partly because of “citation in-breeding”—the repeated citation of the same few selected examples from tropical avifaunas (Rahbek 1995). However, the scientific foundation for this phenomenon in tropical birds (cut to the bone) is a single, careful study from the Peruvian Andes, which apparently showed a monotonic decline in species richness with increasing elevation (Terborgh 1977; see also Terborgh 1971, 1985; Terborgh and Weske 1975). This generalization should have been viewed with skepticism, because Terborgh (1977) stressed that when sampling effort was standardized, the species-richness curve was hump shaped rather than monotonic.

The view that the elevational gradient of species richness resembles the latitudinal gradient (e.g., MacArthur 1972; Brown 1988) was strongly advocated in an article by Stevens (1992), who stated that “biologists have long recognized that elevational and latitudinal species-richness gradients mirror each other” (p. 899). Accordingly, we would expect a monotonic decrease in species richness with increasing elevation to be the general pattern. However, most examples provided by Stevens actually show a minor hump at intermediate elevation, as correctly pointed out by Colwell and Hurtt (1994). A quantitative review of available data sets showed that although a decline in species richness with elevation seems a general trend, hump-shaped distributions are more typical than monotonic declines—a pattern independent of region, scale, and taxon (Rahbek 1995).

Interpretation of species-richness gradients is complicated by area effect. The influence of area on the number of species has been called “one of community ecology’s few genuine laws” (Schoener 1976, p. 629). Nevertheless, most studies dealing with variation in species richness along elevational gradients have not dealt with the effect of area (see review in Rahbek 1995), although some studies have (e.g., Whittaker and Niering 1975; Thiollay 1980; Lawton et al. 1987). This article presents the results of a regional analysis of avian species richness along elevational gradients where the influence of area has been factored out. The analysis is based on all land bird species occurring in the tropical biomes of South America (i.e., more than one-quarter of the extant species of birds on Earth).

MODELS

Climatic, biological, and historical explanations have been put forward in analyses of elevational gradient patterns without considering appropriate null models (Colwell and Hurtt 1994). Ad hoc explanations have been offered for results diverging from the traditionally expected decline of species richness with elevation, for example, postulating abnormal local hot spots of resources (see, e.g., Terborgh 1977). Here I examine four models of species-richness variation along elevational gradients (for discussions of other hypotheses, see Lawton et al. 1987; McCoy 1990).

Model 1: The Species Richness/Primary Productivity Pattern Is Monotonic

A monotonic change in species richness along latitudinal and elevational gradients reflects climatic variables and resultant decreasing productivity (e.g., Simpson 1983), which declines away from the equator and sea level (fig. 1A).

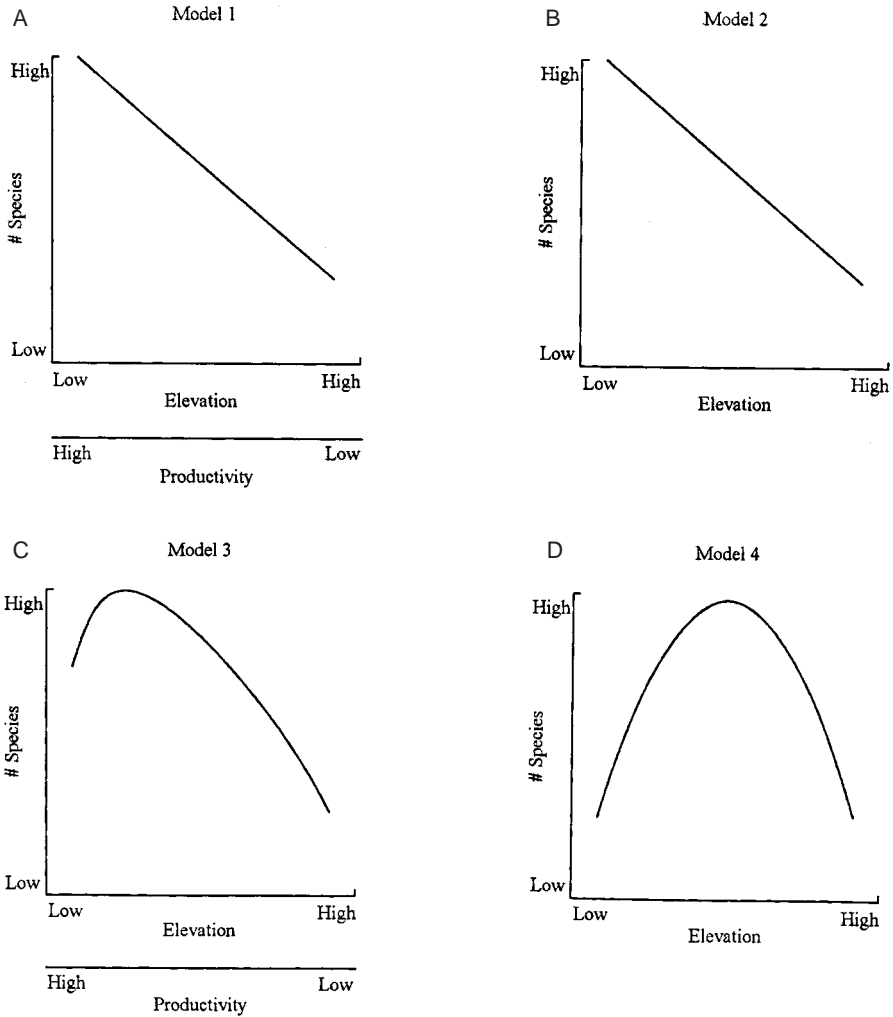


FIG. 1.—Four graphic models of elevational variation in species richness. Model 1, a monotonic species richness/productivity pattern (A); model 2, Rapoport's rule (B); model 3, a hump-shaped species richness/productivity pattern (C); and model 4, bounded random geographical ranges with two hard boundaries (D).

A positive correlation between productivity and species richness has been based on theories involving mechanisms by which increased availability of energy often results in the proliferation of species rather than increased populations of existing species (e.g., Hutchinson 1959; Preston 1962; Connell and Orias 1964; MacArthur 1965, 1969, 1972; Brown and Gibson 1983; Wright 1983; Brown 1988; Currie 1991). Abrams (1988) found that productivity from a theoretical point of view could lead to a monotonic rise in species richness (but for criticism, see Tilman and Pacala 1993; for a reply, Abrams 1995).

A decrease in productivity from sea level to mountaintop is the classical view

used in studies of tropical avian communities (see, e.g., MacArthur 1969; Orians 1969, 1994; Terborgh 1971, 1977; Terborgh and Weske 1975). Actual evapotranspiration (i.e., total evaporation plus transpiration, which equals the precipitation minus the percolation and runoff) is closely and positively correlated with net aboveground productivity (Rosenzweig 1968; see also Major 1963; Lieth and Whittaker 1975). The fact that evapotranspiration is greater in tropical lowlands (Holdridge 1967) suggests that productivity is also highest at the low elevations. Latham and Ricklefs (1993) used similar reasoning in their study of the relationship between tree species richness in moist forests and available energy (see also Lonsdale 1988; O'Brien 1993).

The supposedly negative monotonic relationship between elevation and species richness has been used as support for the existence of a positive relationship between species richness and productivity (Orians 1969; MacArthur 1972; Terborgh 1977; Simpson 1983). However, this logical extrapolation cannot be accepted until the effect of area on species richness is adequately accounted for (see also Terborgh 1973).

Model 2: Rapoport's Rule

According to Rapoport's rule (Stevens 1989, 1992; see also Rapoport 1975, 1982), the mean elevational range (and mean latitudinal range) of species increases with increasing elevation. Stevens (1989, 1992) suggested that this was a reflection of an increase in amplitude of ecologically important climatic variables with elevation (as with latitude). Although Rapoport's rule ignores productivity as the important factor, it is somewhat related to model 1 by suggesting that the patterns of species richness along latitudinal and elevational gradients are caused by parallel variation of climatic variables.

The result is a mass effect (*sensu* Shmida and Whittaker 1981) in the lowland, where greater species richness is caused by an infusion of species from nearby lowland areas. Such species are capable of surviving in the lowlands because of the proximity of nearby lowland core areas (the rescue effect of Brown and Kodric-Brown 1977; see also Rosenzweig 1975; Shmida and Wilson 1985) but are unable to maintain their populations outside core areas (the Rapoport-rescue hypothesis of Stevens 1989, 1992). Hence, lowlands should represent sink habitats (*sensu* Shmida and Ellner 1984; see also Pulliam 1988) for a higher number of species than do mid- and high-elevational zones (Stevens 1992).

The increase in the mean elevational range of species with elevation should result in a parallel, monotonic decrease of species richness with elevation caused by narrower environmental tolerance of genuine lowland species (fig. 1B).

Model 3: The Species Richness/Productivity Pattern Is Hump Shaped

An increase in species richness with productivity is by no means universal (e.g., Rosenzweig 1971; Tilman 1982, 1993; Abramsky and Rosenzweig 1984; Carson and Barrett 1988; Begon et al. 1990). Much empirical evidence for hump-shaped regional patterns has accumulated in recent years (Rosenzweig and Abramsky 1993; Rosenzweig 1995), and patterns of species richness versus elevation have been used to support this model (Rosenzweig 1992, 1995; Rosenzweig and Abramsky 1993).

According to this empirically derived model, species-richness peaks at some intermediate elevation near the lower end of the elevational scale but decreases at the presumably most productive end of the elevational gradient near sea level (fig. 1C). This model assumes, as model 1 does, that productivity decreases monotonically with elevation (see model 1 for justification). Whereas the hypotheses to explain the increase in species richness with productivity are equal to those of model 1 (see discussion of model 1 for references), the decrease phase at the highest level of productivity still remains a puzzle (Rosenzweig 1995). Of the nine different hypotheses proposed in the literature to explain the decrease phase (reviewed in Rosenzweig 1995; see also Rosenzweig and Abramsky 1993), two have been highlighted as the currently most plausible hypotheses (Rosenzweig 1995): reduction in the covariance of population densities (i.e., high temporal covariance among species leads to higher richness, but as productivity increases, the covariance diminishes) and intertaxonomic competition (i.e., competition among taxa causes the decrease). Both hypotheses may pertain to the elevational gradient. However, the first one presently relies entirely on theory, whereas the second one lacks a mechanistic model, making it poor for predictions, although it does predict that the position of the peak of species richness on the productivity axis should vary from taxon to taxon (Rosenzweig 1995).

Model 4: Bounded Random Geographical Ranges (Two Hard Boundaries)

In this model, the pattern of species richness arises from the assumption of a random elevational association between the size and placement of elevational ranges of species (Colwell and Hurtt 1994). This model assumes that the elevational gradient is bounded by two hard boundaries beyond which species' ranges do not extend. For Neotropical land birds, these two hard boundaries are represented by sea level and the tallest Andean peaks (>6,500 m or perhaps the lower limit of the permanent snow line at ca. 5,000 m). The potential elevational range of any land bird species lies within these end points.

If range values are generated as a bivariate, uniform random coverage of feasible values, and if there is no constraint in the maximum elevational range of each species other than those set by the hard boundaries, species-richness peaks at the median elevational gradient (similar to that described in Colwell and Hurtt's [1994] model 2). Further constraints in the maximum elevational range lower this peak and create a plateau at midelevation centered around the median of the elevational gradient (see figs. 3 and 4 in Colwell and Hurtt 1994). However, the model chosen here is regarded by Colwell and Hurtt (1994, p. 581) as the "most realistic null model" for gradients with two hard boundaries and a minimum of biological assumptions.

According to this variant of Colwell and Hurtt's null models, the number of species will peak at midelevation, with a symmetrical decrease in species richness toward the two end points (fig. 1D).

CHOICE OF TAXA AND REGION

Most studies of the elevational gradient have been conducted on tropical rather than temperate organisms (Rahbek 1995), and I follow this tropical trend

here. Birds seem an obvious choice because the generalization of a monotonically declining pattern of species richness with elevation was based primarily on studies of tropical birds on both local and regional scales (Rahbek 1995). Moreover, birds are the only group of organisms for which we have sufficient knowledge of geographical and elevational distributions in the Tropics. Nearly all studies dealing with continental (Moreau 1966; Orians 1969; Pearson and Ralph 1978; Stiles 1983; Graham 1990; Navarro 1992; Stevens 1992) and island avifaunas (Kikkawa and Williams 1971; Diamond 1972; Lack 1976; Beehler 1981) found species richness to decline monotonically with elevation. None of these avian studies considered the effect of area carefully.

South America, the most species-rich continent for birds, serves as an illustrative example. The Amazonian lowlands are famous for their species richness and are believed to have the world's highest level of regional species richness for birds (Amadon 1973) and of single-point species richness (Remsen and Parker 1983, citing data in Pearson 1977). However, the regional species richness could simply be a result of the enormous area of the lowlands (Terborgh 1973). Perhaps the lowlands are as depauperate as other elevational zones when the influence of area is considered. In this article, the potential latitudinal effect on the elevational pattern (e.g., that mountains might be "higher" in the Tropics, sensu Janzen 1967) has been reduced by restricting the analysis to land birds in tropical biomes of South America as defined by Hueck and Seibert (1972).

METHODS

At a regional level, the influence of area (denoted A) on the relationship between the number of species (denoted S) and elevation was studied by determining S/A curves for different elevational zones. ANCOVA on the effect of elevation on richness, with area as a covariate, was used to test for differences in species richness between elevational zones using a Tukey pairwise comparison test (Zar 1984). I assumed that only regression lines of S/A curves slopes not differing significantly from each other were comparable.

The analysis of S/A curves is fraught with methodological problems and has provoked heated discussion (e.g. Connor and McCoy 1979; Sugihara 1981; McGuinness 1984; Williamson 1988; Lomolino 1989). Among the possible methods, I used least-squares linear regression because it provides better opportunities to extract a larger variety of useful information than do other methods (Fry 1993a). Before comparing slopes, I tested four models of S/A curves (discussed in Connor and McCoy 1979): S/A , $S/\log A$, $\log S/A$, and $\log S/\log A$. The choice of S/A model was based on comparison of r values (see Connor and McCoy 1979) and fulfillment of assumptions, including comparison of the corresponding statistical tests. ANOVA and ANCOVA were used to evaluate data. The assumptions of least-squares linear regression, ANOVA, and ANCOVA were tested following the procedure suggested by Fry (1993a, 1993b), that is, normal distribution, homoscedasticity of variance of residuals, normal distribution and mutual independence of the errors of y , autocorrelation and correlation between residuals, and large influence of individual data points on the slope of

the regression (see also Zar 1984). The SYSTAT statistic package, version 5.03 for Windows, was used (SYSTAT 1992).

Components of Elevational S/A Curves

For each species two parameters were noted: geographical range and elevational range. Samples from areas of different size are required from each elevational zone to create *S/A* curves necessary for factoring out the influence of area. Countries of different sizes were chosen as units for analysis of geographical distribution. Although these geopolitical units are not comparable on the basis of size and shape (Graves and Gotelli 1983), they are often the only choice in broad-scale biogeographical analysis, especially when dealing with nearly 3,000 species, many of which are poorly known.

The elevational gradient was divided into seven zones: 0–500 m, 500–1,000 m, 1,000–1,500 m, 1,500–2,000 m, 2,000–3,000 m, 3,000–4,000 m, and $\geq 4,000$ m. The shift from 500-m to 1,000-m intervals above 2,000 m was determined by the level of topographic accuracy prevalent on available maps. Because of the increasing steepness of the terrain, this may bias the comparison of low- and midelevational zones (<2,000 m) with high-elevational zones (>2,000 m). However, the expected hump on the species-richness curve of model 3 is within the range of the 500-m intervals. Furthermore, according to all four models, we would expect a decline in species richness at higher elevations.

The geographical distribution of a species is noted by its presence or absence in each country. The area of each elevational zone in each geographical unit (country) and the number of species per zone in each country were used to create *S/A* curves for each of the seven elevational zones.

Species Included

The taxonomy of South American birds is under extensive revision. I adopted the species-level taxonomy of Sibley and Monroe (1990, 1993), which reflects a subjective “traditional” taxonomy (see Siegel-Causey 1992). A total of 3,087 species (including seabirds and vagrants) has been recorded in South America (excluding species known only from the Galápagos and Juan Fernández Islands). My analyses were limited to land birds, conservatively defined as terrestrial species and species restricted to fresh water or partially using such habitats, of the tropical biomes of South America. I excluded non-land bird species, species occurring exclusively outside tropical South America, island endemics, vagrants, introduced species, and resident species known only from a few records, reducing the number to 2,801.

Distribution Data

Information on elevational range was taken mainly from the database of Parker et al. (1996). In the few instances in which elevational information was lacking, elevational ranges were determined from information in the literature and by personal communication with experts on South American birds (especially J. Fjeldså, G. Graves, and R. S. Ridgely).

The elevational ranges exclude records lying outside the typical range of the

species. The majority of such elevational outliers are records of lowland or highland species occasionally occurring in midelevational zones. By discarding these records when measuring a species' elevational range, one favors the hypotheses that predict a steady decline of species richness with elevation (i.e., models 1 and 2) in contrast to the hump-shaped curve (models 3 and 4). Elevational ranges of species were adjusted for each country if the ranges were known to be different. In general, Andean bird species show a remarkable consistency of elevational distribution over wide latitudinal ranges (Chapman 1926; Graves 1985; Remsen and Cardiff 1990).

Tropical South America experiences a yearly influx of migratory species primarily from North America and a seasonal movement of South American nonbreeding species. The role and influence of these migrants on community structure and processes are poorly known. It has been suggested that migrants can be considered full members of tropical communities rather than temporary intruders (e.g., Rabøl 1987). Information on breeding status and geographical distribution was taken directly from the same database as the elevational ranges (Parker et al. 1996), supplemented with information in the literature and personal communication (especially J. Fjeldså, G. Graves, and R. S. Ridgely). Thus, it was noted whether species were permanent residents or nonbreeding migrants. Analyses were performed with and without migrant species. Ninety species were classified as migrants only.

Calculation of Area

Bartholomew's azimuthal equal-area projection maps, scale 1:5,000,000, were used to calculate area. For each country, the boundaries of each elevational zone were traced on transparent sheets. Tracings were then placed over grid paper (40.2 km²/square). The area of a particular elevational zone was estimated (0%, 50%, 100% coverage) for each grid and then summed across all squares and rounded to the nearest 1,000 km². The total area of tropical South America is 14,727,000 km² (ca. 368,000 grids). Table 1 summarizes the database.

As do most other studies of the effect of area on species richness, this study assumed that area was proportional to the measured area of a flat map. This traditional approach neglects topographic variation. On an elevational gradient, area is by this procedure likely to be underestimated because of the slope at various elevations. To test for this potential bias, I repeated all the Tukey pairwise comparison tests in a scenario in which the 0–500-m zone was assumed to be totally flat, whereas all other zones were assumed to have a uniform slope of 45° (i.e., the area of all zones except the 0–500-m zone was multiplied by 1.41). Here it is worth remembering that it is not ground area per se that determines species richness. A more appropriate measurement of area might be the volume of available habitat, and the slope bias is likely offset somewhat by the fact that vegetation height decreases monotonically with elevation.

Species Turnover Rate and Possible Biases

The null model (model 4) incorporates the constraints introduced on the elevational gradient by the two hard end points (boundaries). For a more detailed

TABLE 1

DATA FOR THE SPECIES-AREA CURVES FOR TROPICAL SOUTH AMERICAN LAND BIRDS

	French Guinea	Surinam	Guyana	Venezuela	Colombia	Ecuador	Peru	Bolivia	Chile*	Argentina*	Paraguay*	Brazil*	Total
0-500 m:													
Area	91	155	198	685	874	150	638	649	11	492	369	6,537	10,849
S	595	633	663	939	1,093	906	1,047	960	139	666	624	1,420	1,913
S _B	562	584	614	864	1,011	835	956	908	115	631	573	1,351	1,836
500-1,000 m:													
Area	...†	8‡	14‡	152	72	26	94	49	15	42	3‡	1,681	2,156
S	...	566	615	752	894	798	989	892	128	643	591	1,182	1,802
S _B	...	522	575	702	817	741	906	841	107	611	544	1,116	1,725
1,000-1,500 m:													
Area†	2‡	48	52	15	59	39	28	16	...†	117	376
S	422	660	766	670	744	710	123	527	...	852	1,511
S _B	390	618	695	607	661	666	103	499	...	794	1,441
1,500-2,000 m:													
Area†	19	63	19	80	29	17	8	...	4‡	239
S	521	653	572	629	485	126	388	...	434	1,054
S _B	487	588	513	568	445	99	361	...	384	992
2,000-3,000 m:													
Area	5	52	33	113	63	14	15	295
S	322	586	517	624	455	126	289	914
S _B	298	526	476	579	428	108	267	869
3,000-4,000 m:													
Area	2	23	22	137	186	38	51	459
S	90	217	230	364	273	126	169	457
S _B	80	203	220	348	265	119	162	448
≥4,000 m:													
Area†	3	5	164	83	43	55	353
S	20	17	53	133	119	84	92	149
S _B	17	17	50	127	117	82	91	148
Total tropical area	91	163	214	911	1,139	270	1,285	1,098	166	679	372	8,339	14,727

NOTE.—Areas are given in 1,000 km²; S = all land bird species, including nonbreeding, and S_B = all breeding land bird species.

* Only the tropical part of the country is included.

† Figure is <1,000 km² and therefore not considered.

‡ Figure is based solely on species' general distribution in South America and is thus likely an overestimate.

exploration of how these constraints may influence the species-richness pattern, I analyzed the pattern of turnover rate between adjacent zones on the elevational gradient using Whittaker's (1960) beta index: $\beta = S/\alpha - 1$, where S is the total number of species in two adjacent zones and α is the average species richness of any pair of zones. Whittaker's beta index has been shown to be superior to other more recent alternative measures (review in Wilson and Shmida 1984; Magurran 1988; but see also Harrison et al. 1992). The other indexes of turnover rate reviewed by Wilson and Shmida (1984) would give other values but similar patterns, though the derivations of the associated measures are quite different. Spearman rank correlation was used to test for significant trends in turnover rate with elevation, and Kolmogorov-Smirnov one-sample tests were used for the assumption of constancy in elevational turnover rate within a country. All tests in this article are two-tailed unless otherwise stated.

Geographical turnover rates could bias the analysis of the pattern if turnover rates within the same elevational zone, for several countries, varied significantly from those of other elevational zones. Thus, a significantly higher geographical turnover rate within one elevational zone could perhaps cause that particular zone to appear, spuriously, to be the most species rich overall. An index of faunal similarity between corresponding elevational zones of adjacent countries was calculated using Sørensen's (1948) similarity coefficient index: $C_s = 2j/(a + b)$, where j equals the number of species shared between two zones and a and b are the number of species in each zone. Sørensen's index was chosen among other similarity indexes based on the review of these by Magurran (1988). A Kruskal-Wallis test was used to test whether median indexes for each elevational zone were equal.

A pairwise test for differences in indexes of geographical turnover rate between any combination of two elevational zones was conducted using Mann-Whitney U -tests and Student's t -tests. Similar tests were also carried out on one set of indexes adopting Whittaker's (1960) equation for community turnover: $S_T = S/\bar{\alpha} - 1$, where S is the total number of species recorded in a given elevational zone within tropical South America and $\bar{\alpha}$ is the average number of species found within the given elevational zone in each country.

Statistical tests on these similarity and turnover rate indexes might be influenced in an unpredictable way by the inclusion of Brazilian data, partly owing to the enormous size of the country, partly because birds of the Brazilian uplands are disjunctly distributed, often far from Andean and Guianan highlands, and because Brazil mainly borders other countries with Amazonian lowlands. Furthermore, the Colombia-Peru combination also differs from the rest of the data, as these two countries share only a small border segment in the Amazon lowlands, while their Andean ranges are far apart. Therefore, separate tests are conducted on subsamples that exclude Brazil and the Colombia-Peru combination.

The two lowest elevational zones of the Chilean part of the study are extremely dry, consisting largely of desert (Hueck and Seibert 1972), and support very few bird species (table 1). These zones are not comparable with lowland zones of other countries. Higher-elevational zones in Chile are biologically more

similar to those in adjacent countries. However, I excluded Chile from the analyses to reduce the risk of biases (toward a midelevational hump) and to standardize the data.

RESULTS

Of the four species-area models investigated, only $S/\log A$ and $\log S/\log A$ fulfilled all statistical assumptions (mentioned in Methods). Both seemed to fit the data set equally well, but the latter was chosen solely because it is traditionally applied in most S/A studies (Connor and McCoy 1979), and thus my results would be comparable with the bulk of species-area literature.

The Pattern of Species Richness along the Elevational Gradient

Illustrating species-area curves on the bivariate plot allowed visual comparison of the species richness of separate elevational zones (fig. 2A). Analyses were also conducted on a subsample of countries that excluded Brazil with its enormous lowland area (fig. 2B) and on a subsample of the four Andean countries (Colombia, Ecuador, Peru, and Bolivia) to test for robustness in the pattern (fig. 2C). These latter countries share a common historical and geographical background within the tropical zone, the Andes running continuously through all four countries, with all seven elevational zones represented. However, the small sample size ($n = 4$) precludes powerful statistical tests, and a single data point may influence the regression. All plots were based on breeding and nonbreeding species (see also table 2). Corresponding plots excluding nonbreeding species were nearly identical. The regression lines of the 500–1,000-m zone were elevated above those of the 0–500-m zone for all these sampling groups (fig. 2; table 2).

Considered as a group, regression slopes were significantly different (ANCOVA, $F = 4.560$, $P = .001$, excluding Chile; $F = 3.170$, $P = .014$, excluding Chile and Brazil). However, pairwise Tukey tests revealed that statistical significance was due to the influence of the $\geq 4,000$ -m elevational zone. The z value of the $\geq 4,000$ -m zone (0.43) resembled high values typically found for S/A curves from islands (Williamson 1988; see also Vuilleumier 1970), whereas the slopes for the other elevational zones fell within a restricted range (0.12–0.26) more typical for species-area curves from mainland areas (fig. 2A). When the $\geq 4,000$ -m zone was excluded, the ANCOVA was not significant for subsamples excluding Chile ($F = 1.723$, $P = .154$) and both Chile and Brazil ($F = 1.024$, $P = .420$). An additional round of Tukey tests revealed that among the remaining six zones, only the slope of the 3,000–4,000-m zone was significantly different from those of the 500–1,000-m and 1,000–1,500-m zones ($P < .05$). For the small group of the four Andean countries, no differences were found when all seven elevational zones were included ($F = 2.045$, $P = .127$; excluding the $\geq 4,000$ -m zone, $F = 0.154$, $P = .975$).

The results of the Tukey pairwise comparison test show that, when area is factored out, on a continental scale, species richness in the 0–500-m zone was surpassed by that of midelevational zones, with a significantly higher species richness in the 500–1,000-m zone ($P < .005$) (fig. 2A; table 3). Species richness

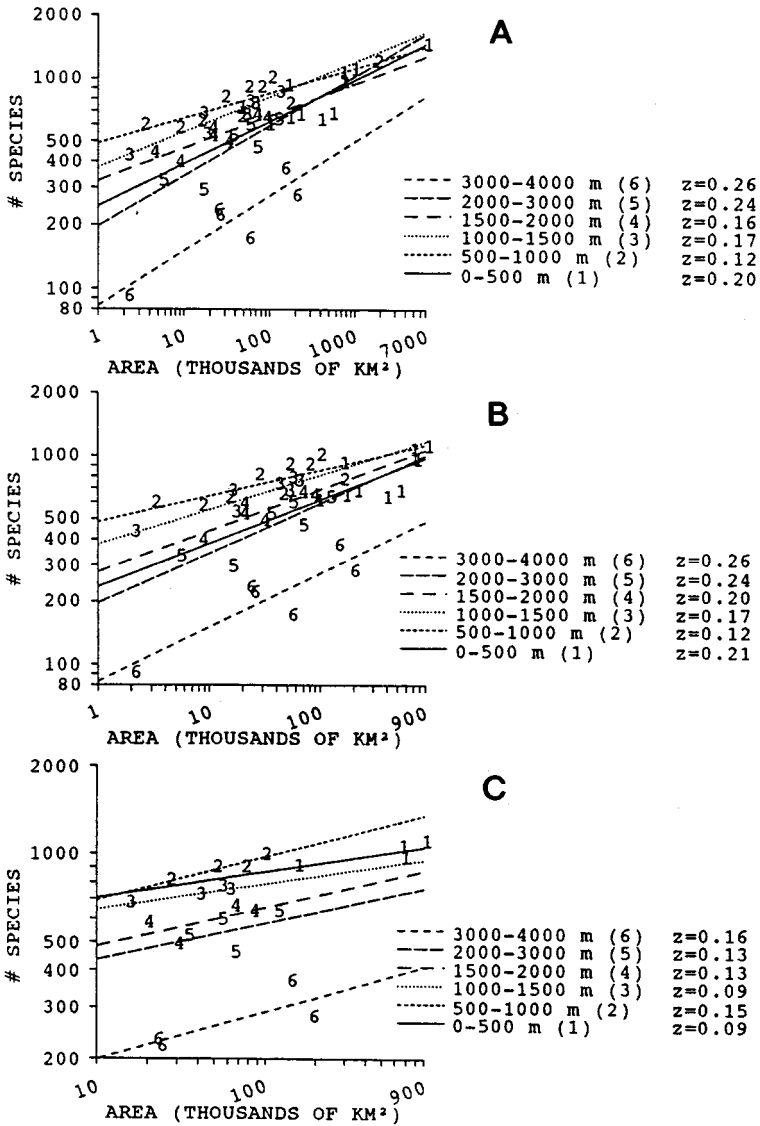


FIG. 2.—Relationship between species richness of South American tropical land birds (breeding plus nonbreeding) and elevation on a regional scale showed by regression lines for each elevational zone. The $\geq 4,000$ -m zone was excluded; its regression line lay significantly below those of the other zones. Numbers refer to the elevational zone of each data point; z = the slope of a double-log plot. A was based on data excluding Chile, B excluded data from Chile and Brazil, and C included only data from Colombia, Ecuador, Peru, and Bolivia. Values for the $\geq 4,000$ -m zone were $z = 0.43$ for the data of A and B and $z = 0.44$ for C. Notice that the scales of the X- and Y-axes are different in the three figures.

TABLE 2
LOG S-LOG A REGRESSION AND CORRELATION VALUES FOR EACH ELEVATIONAL ZONE FOR THREE DIFFERENT SAMPLES

	ALL COUNTRIES EXCEPT CHILE		ALL COUNTRIES EXCEPT CHILE AND BRAZIL		ANDEAN COUNTRIES (i.e., Colombia, Ecuador, Peru, and Bolivia)	
	r^2	r_s	r^2	r_s	r^2	r_s
0-500 m	.67 ^{F=1845, df=1, 9***}	.85****	.48 ^{F=727, df=1, 8*}	.81****	.71 ^{F=482, df=1, 2}	1.00 ^{NT}
	.69 ^{F=2002, df=1, 9***}	.85****	.48 ^{F=742, df=1, 8*}	.81****	.83 ^{F=984, df=1, 2}	1.00 ^{NT}
500-1,000 m	.74 ^{F=2216, df=1, 8***}	.84****	.58 ^{F=948, df=1, 7**}	.78**	.90 ^{F=1826, df=1, 2}	1.00 ^{NT}
	.76 ^{F=2547, df=1, 8***}	.83****	.60 ^{F=1065, df=1, 7**}	.77**	.82 ^{F=885, df=1, 2}	.80 ^{NT}
1,000-1,500 m	.88 ^{F=4485, df=1, 6***}	.86****	.85 ^{F=2839, df=1, 5***}	.79*	.86 ^{F=1212, df=1, 2}	.80 ^{NT}
	.91 ^{F=5909, df=1, 6***}	.86****	.88 ^{F=3752, df=1, 5***}	.79*	.80 ^{F=789, df=1, 2}	.40 ^{NT}
1,500-2,000 m	.74 ^{F=1440, df=1, 5**}	.83**	.77 ^{F=1304, df=1, 4*}	.76	.45 ^{F=161, df=1, 2}	.60 ^{NT}
	.79 ^{F=1899, df=1, 5***}	.83**	.77 ^{F=1310, df=1, 4*}	.76	.49 ^{F=195, df=1, 2}	.60 ^{NT}
2,000-3,000 m	.72 ^{F=1010, df=1, 4*}	.77	.72 ^{F=1010, df=1, 4*}	.77	.21 ^{F=53, df=1, 2}	.40 ^{NT}
	.74 ^{F=1112, df=1, 4*}	.77	.74 ^{F=1112, df=1, 4*}	.77	.29 ^{F=82, df=1, 2}	.40 ^{NT}
3,000-4,000 m	.79 ^{F=1487, df=1, 4**}	.71	.79 ^{F=1487, df=1, 4**}	.71	.63 ^{F=341, df=1, 2}	.60 ^{NT}
	.81 ^{F=1686, df=1, 4**}	.71	.81 ^{F=1686, df=1, 4**}	.71	.67 ^{F=399, df=1, 2}	.60 ^{NT}
≥4,000 m	.85 ^{F=1643, df=1, 3*}	1.00*	.85 ^{F=1643, df=1, 3*}	1.00*	.84 ^{F=1036, df=1, 2}	1.00 ^{NT}
	.86 ^{F=1821, df=1, 3*}	1.00*	.86 ^{F=1821, df=1, 3*}	1.00*	.85 ^{F=1142, df=1, 2}	1.00 ^{NT}

NOTE.—The first line gives data when all species are included; the second line, when only breeding species are included. Also, r^2 is the coefficient of determination (tested by ANOVA) with F (regression df, residual df) values (n = residual df + 2), r_s is the Spearman rank-correlation coefficient (one-tailed), and NT = nonstable (i.e., sample size was too small).

* $P < .05$.
** $P < .02$.
*** $P < .01$.
**** $P < .005$.

TABLE 3

MATRIX OF TUKEY PAIRWISE COMPARISON PROBABILITIES COMPARING LOG SPECIES RICHNESS BETWEEN ELEVATIONAL ZONES WITH LOG AREA AS A COVARIATE IN AN ANCOVA, AFTER EXCLUDING THE $\geq 4,000$ -m ZONE

	0–500 m	500– 1,000 m	1,000– 1,500 m	1,500– 2,000 m	2,000– 3,000 m	3,000– 4,000 m
4,000–3,000 m:						
A						1.000
B						1.000
C						1.000
3,000–2,000 m:						
A					1.000	.000
B					1.000	.000
C					1.000	.000
2,000–1,500 m:						
A				1.000	.189	.000
B				1.000	.311	.000
C				1.000	.525	.000
1,500–1,000 m:						
A			1.000	.273	.001	.000*
B			1.000	.244	.001	.000*
C			1.000	.033	.001	.000
1,000–500 m:						
A		1.000	.923	.031	.000	.000*
B		1.000	.860	.016	.000	.000*
C		1.000	.239	.000	.000	.000
500–0 m:						
A	1.000	.004	.095	.985	.613	.000
B	1.000	.002	.059	.936	.909	.000
C	1.000	.473	1.000	.308	.022	.000

NOTE.—Results, based on all species, are shown for three subsamples of countries: A = all countries except Chile; B = all countries except Chile and Brazil; C = Andean countries (Colombia, Ecuador, Peru, and Bolivia). Numbers in boldface italics indicate that the regression line of the elevational zone in the column lies significantly higher (i.e., zone is more species rich) than does the regression line of the elevational zone in the row; numbers in boldface alone indicate a significantly lower position of regression line.

* Slopes are significantly different ($P < .05$).

in the 1,000–1,500-m zone was also higher than that in the 0–500-m zone (fig. 2A), but not significantly so ($P < .10$; table 3). The pattern was the same when Brazil was excluded from the analysis (fig. 2B; table 3). Despite the fact that the 500–1,000-m zone of the four Andean countries had the highest regression line (fig. 2C), it was not significantly more species rich than the 0–500-m zone ($P < .50$; table 3).

The level of significance of all the significant figures (i.e., $P < .05$) given in table 3 would be the same if tested by a Bonferroni pairwise procedure with probabilities adjusted for 15 comparisons, although nonsignificant figures may vary. Also, with slope-corrected area (see *Calculation of Area*), all significant figures of table 3 remained significant (i.e., $P < .05$), although the P value changed slightly for some figures.

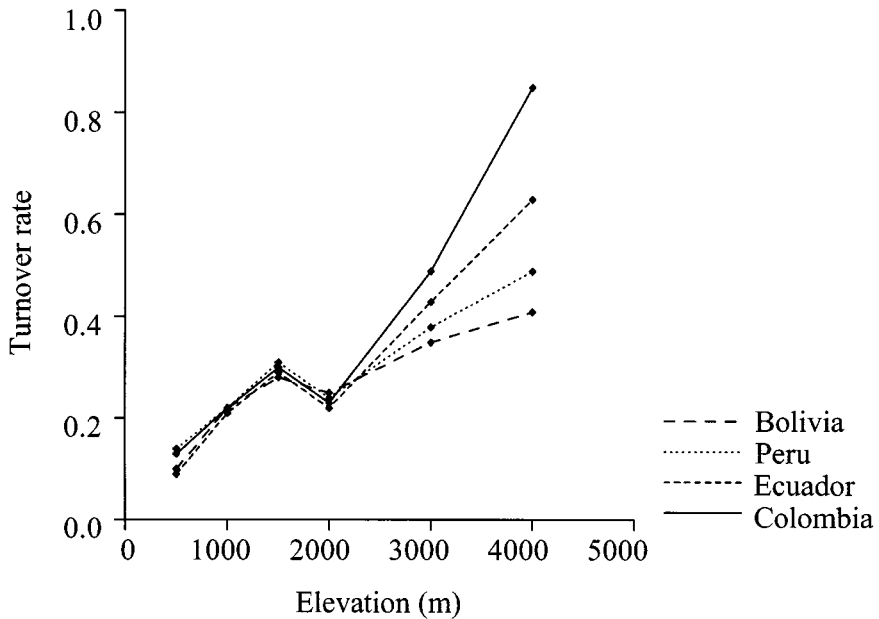


FIG. 3.—Turnover rate over the elevational gradient calculated on a data set including breeding and nonbreeding species using the beta turnover index of Whittaker (1960) for Colombia ($r_s = .94$; $P < .02$), Ecuador ($r_s = 0.94$; $P < .02$), Peru ($r_s = 0.94$; $P < .02$), and Bolivia ($r_s = 0.94$; $P < .02$).

Elevational Turnover Rates

Turnover rate of species between elevational zones within each of the Andean countries was positively correlated with elevation (fig. 3; table 4) but was not constant over the elevational gradient (Kolmogorov-Smirnov one-sample test, $P < .05$ for all four countries, $df = 5$). Some constraints exist in the data because many species have the same elevational range in more than one country. However, the turnover pattern for each country was remarkably similar considering the latitudinal range of Andean countries.

The 0–500-m zone was the only zone having a noticeable number of species with restricted elevational ranges (table 4). Many of these were water birds or species restricted to habitats that only occur near sea level. Notice that the 0–500-m zone and the 500–1,000-m zone share many species but that the 500–1,000-m zone shares more species with higher-elevational zones.

Geographical Turnover Rates

The medians of Sørensen's similarity indexes within each elevational zone among countries were not significantly different (Kruskal-Wallis test, $P = .919$, $df = 6$). The corresponding results on the different subsamples of countries (i.e., excluding Brazil, $P = .437$; excluding Brazil and the combination of Colombia-

TABLE 4
 NUMBER OF SPECIES (ALL SPECIES INCLUDED) SHARED AMONG ELEVATIONAL ZONES
 IN COLOMBIA (C), ECUADOR (E), PERU (P), AND BOLIVIA (B)

	0–500 m	500– 1,000 m	1,000– 1,500 m	1,500– 2,000 m	2,000– 3,000 m	3,000– 4,000 m	≥4,000 m
≥4,000 m:							
C							0
E							1
P							6
B							4
4,000–3,000 m:							
C						8	17
E						4	52
P						9	127
B						3	115
3,000–2,000 m:							
C					12	199	12
E					6	213	39
P					14	305	77
B					3	238	86
2,000–1,500 m:							
C				1	477	107	7
E				0	427	129	25
P				1	475	170	45
B				0	353	139	41
1,500–1,000 m:							
C			9	495	322	70	7
E			5	439	294	76	22
P			3	476	323	122	38
B			0	432	300	107	34
1,000–500 m:							
C		1	644	382	215	46	7
E		0	580	354	214	53	20
P		3	676	411	264	95	35
B		1	626	348	222	81	32
500–0 m:							
C	224	869	620	363	200	44	7
E	130	776	558	336	200	51	19
P	172	875	565	319	193	83	33
B	127	833	568	300	182	76	31

NOTE.—Numbers in the diagonal represent the number of species restricted to this zone.

Peru, $P = .631$; including only the Andean subset, $P = .963$) or when nonbreeding species were excluded were very similar and also not significant.

There were no significant differences in geographical turnover rate among elevational zones (table 5). Thus, the relationship between species richness and elevation does not seem to be caused by differences in geographical turnover rate between elevational zones. Similarly, no significant elevational trend in regional turnover of species among countries could be found when using Whittaker's beta index of turnover instead of Sørensen's similarity index (Spearman rank test, two-tailed). Because the numbers used for this test were based on subsam-

TABLE 5
COMPARISON OF SØRENSEN'S SIMILARITY INDEXES AMONG ELEVATIONAL ZONES,
EXCLUDING CHILEAN DATA

	0-500 m	500-1,000 m	1,000-1,500 m	1,500-2,000 m	2,000-3,000 m	3,000-4,000 m	≥4,000 m
0-500 m		.918	.740	.397	.807	.761	.277
		.891	.528	.324	.799	.959	.321
500-1,000 m	.652		.659	.393	.789	.947	.351
	.703		.612	.370	.707	.874	.335
1,000-1,500 m	.445	.341		.772	.403	.628	.587
	.355	.612		.602	.426	.583	.391
1,500-2,000 m	.421	.421	1.000		.481	.450	.733
	.521	.867	.639		.269	.369	.486
2,000-3,000 m	.140	.203	.520	.292		.808	.582
	.199	.321	.507	.325		.868	.295
3,000-4,000 m	.219	.159	.455	.462	.916		.581
	.216	.344	.539	.351	.971		.319
≥4,000 m	.394	.536	1.000	1.000	1.000	1.000	
	.331	.379	.449	.395	.579	.570	

NOTE.—The top diagonal gives the probability values (*P*) for all possible combinations (i.e., all data included), and the bottom diagonal gives the probability values (*P*) when all combinations including Brazil and the Columbia-Peru combination were excluded (see the text). The top value in each cell indicates the result of a Mann-Whitney *U*-test (two-tailed), and the bottom value represents the result of a Student's *t*-test (two-tailed). None of the values were significant at the .05 level.

ples of the same data, further statistical comparison of the data would be inappropriate.

DISCUSSION

The expectation from all four models (see fig. 1) that species richness declines at high elevations was confirmed by the pattern found for South America tropical land birds. The ANCOVA (with area as a covariate), using the Tukey pairwise comparison method, showed that the 3,000-4,000-m zone had significantly fewer species than all other zones (all *P* < .001; table 3). Although the 2,000-3,000-m zone also had significantly fewer species than the 500-1,000-m and 1,000-1,500-m zones (*P* < .001 and *P* = .001, respectively), species richness was not significantly different from that of the 1,500-2,000-m zone or the 0-500-m zone (with the exception of the Andean subsample; *P* = .022). In fact, when the effect of area was factored out, the 0-500-m zone was not significantly more species rich than the 500-1,000-m, 1,000-1,500-m, and 1,500-2,000-m zones (see fig. 2). The 0-500-m zone was actually significantly less species rich than the 500-1,000-m zone, except in the small Andean subsample (see table 3). Thus, the monotonically declining pattern of species richness predicted by models 1 and 2 was not supported (fig. 1A, B). The regional relationship between species richness and elevation tended to be hump shaped, peaking in the 500-1,000-m zone, with a decline above this zone, particularly above 3,000 m (fig. 2; table 3). This pattern resembles that predicted by the null model

(model 4), although the peak was reached at an elevation lower than the median of the gradient, which was in accordance with model 3.

The hump-shaped curve found for tropical South America might be scale dependent. However, even the smaller Andean subsample did not support the hypotheses of a monotonic decline of species richness with elevation (models 1 and 2) (fig. 2C). Instead, the Andean data suggested a more horizontal-linear, if not hump-shaped, relationship between species richness and elevation at the lower end of the gradient, followed by a decrease in species richness at higher elevation.

The pattern in the Andean data raises the question of whether the more pronounced hump-shaped regional pattern found in the two larger data samples might be a result of lumping countries, some of which lack some of the elevational zones. However, this is probably not the case as no significant difference in geographical turnover rate between elevational zones could be detected (table 5). But it is noteworthy that the slope of the regression lines for all elevational zones except the 500–1,000-m zone were considerably lower in the Andean subsample (compare z values of fig. 2C with those of fig. 2A and B). The lack of significant trends in the geographical turnover rates (see, e.g., table 5) suggests that the hump-shaped pattern was not caused by elevational variation in species occurrence. Furthermore, similar elevations support similar species compositions over broad latitudinal ranges, whereas “localities a few hundred meters apart in elevation tend to support different avifaunas” (Remsen and Cardiff 1990, p. 974; see also Terborgh and Weske 1975; Parker et al. 1985). Unfortunately, no relevant data were available from most countries for a more detailed evaluation of the role of elevational turnover rate.

Whereas the null model predicts a symmetrical, hump-shaped pattern of species richness (see fig. 1D), Neotropical land birds showed a tendency toward an asymmetrical hump, with the highest species richness at the lower end of the gradient. The latter is typical for many elevational data sets (based on examination of the raw data reviewed in Rahbek 1995). The challenge is not merely to understand what causes the hump of species richness at midelevation or the decline at high elevations or to explain why species richness of the lowland is much higher than anticipated by the null model. Rather, the real puzzle is why species richness peaks near the lower end of the elevational gradient and declines below this elevation.

The Elevational Gradient as a Productivity Gradient

Rosenzweig and Abramsky (1993) recently concluded that a hump-shaped relationship between species richness and productivity on a regional scale was more typical than a positive monotonic relationship (see also Rosenzweig 1992, 1995). They argued that the elevational gradient in tropical biomes was a good index of productivity and used my rough, preliminary analyses of elevational pattern of species richness for Neotropical land birds (together with other data) to support the hypothesis of a unimodal species richness/productivity pattern (Rosenzweig 1992, pp. 725–726; 1995, pp. 369–370; Rosenzweig and Abramsky 1993, pp. 53–55). The elevational pattern discussed in this article does in-

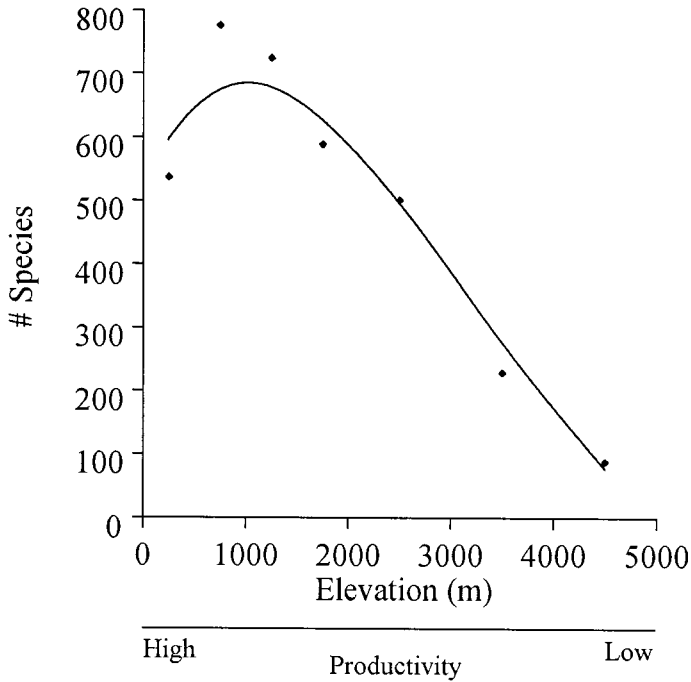


FIG. 4.—Generalized relationship between productivity and species richness, equating the elevational gradient as a productivity gradient. The curve was based on the log/log equations for the data that included all species, excluding data from Chile and setting area = 50,000 km² (see Rosenzweig and Abramsky 1993 for the rationale for using this size of area). Data points were placed at the middle of each elevational zone and at 4,500 m for the $\geq 4,000$ -m zone. The line was fitted by distance-weighted least-squares smoothing.

deed closely resemble the pattern of model 3, in agreement with Rosenzweig and Abramsky's ideas (cf. fig. 1C with fig. 4). However, this interpretation assumes that elevation was a relevant overall indicator of the level of productivity available for birds. Evapotranspiration is tightly correlated with primary productivity (Rosenzweig 1968). Although good supporting data are lacking, evapotranspiration is assumed to decrease with elevation and often presumed to correlate with food availability for birds (Young 1994 and references therein). However, topographical features and environmental parameters can cause the quantity of food available to birds to vary from that predicted by weather data (Janzen 1983).

Another important underlying assumption for the productivity models is that productivity not only generally decreases with elevation but that it decreases monotonically. This is often accepted to be the case, although there is no hard evidence. In a review of the hydrology of moist tropical forests, Bruijnzeel (1990) could find no strong trends indicating that annual evapotranspiration was negatively correlated with elevation in montane forests. In fact, he found that

mean annual evapotranspiration for lower montane forests was “surprisingly close to the mean for lowland forests . . . especially in view of the large difference in average altitude—about 100 m a.s.l. [above sea level] versus about 1750 m a.s.l.—between the two groups” (p. 27). Additionally, forests subjected to frequent or persistent fog or clouds can secure atmospheric moisture through the process of “cloud stripping” (Bruijnzeel 1990). Thus, where fairly stable atmospheric conversions are thought to maintain a stable cloud-forest climate on the border between lowland and harsh highland Andean climates, humidity could influence year-round productivity peaks in certain parts of the Andes at midelevation (e.g., Valencia 1992 and references therein).

The literature on elevational gradients has not reached a consensus concerning how productivity varies with elevation. Some older studies found “unexpected” midelevational humps of species richness, and it was argued that productivity due to local climatic condition was greatest at corresponding intermediate elevations (Janzen 1973; Janzen et al. 1976; Terborgh 1977; see also Chang 1968). Thus, a positive correlation between productivity and species richness was (re-)established (though this is an unsupported assumption).

Although the data on Neotropical birds (fig. 4) agree with the proposed hump-shaped pattern on a regional level (model 3; Rosenzweig and Abramsky 1993), elevation remains a surrogate variable of unknown ability to stand in for productivity.

Impact of Geometric Constraints on the Elevational Gradient

The latitudinal and productivity gradients differ in geometry from that of the elevational gradient. Most significantly, the productivity gradient does not have hard upper and lower boundaries. Whether this is true for the latitudinal gradient is arguable (see Colwell and Hurr 1994), but the latitudinal gradient certainly spans much longer distances than the short elevational gradient. These constraints (i.e., the combination of hard boundaries with a relatively short elevational span) are likely to influence the elevational pattern of species richness, not only as expressed by the null model (fig. 1D) but also through historical and ecological mechanisms that are different in impact from those shaping the productivity and latitudinal gradients.

On the latitudinal gradient, species may have large latitudinal ranges, increasing the chance of allopatric speciation while reducing the chance of extinction (e.g., Rosenzweig 1977, 1992, 1995). By comparison, the elevational slope of the Andes from the lowlands to timberline rarely spans more than 30–50 km (Graves 1985), and the available area per elevational unit tends to decrease with elevation (table 1). The width of the elevational range of a species must exceed a certain minimum to secure a viable local population because of elevational constraints (Graves 1988). Most forest birds of the Andes in Peru have an average width of elevational distribution ranging from 3.7 to 18.3 km (Graves 1988). Because most vertebrates have a much larger latitudinal range than elevational range, we might expect the degree of overlap of species to be higher (per unit of measurement) along the elevational gradient than along the latitudinal gradient. Because the width (i.e., distance along the ground per se) of the elevational gra-

dient is so narrow above the 0–500-m zone, midelevational zones share many species with lower- and higher-elevational zones (table 4).

That the 500–1,000-m zone is the most species rich of the midelevational zones is likely, at least in part, due to its placement adjacent to the large source pool of the 0–500-m zone and to those above it. The number of species shared with the 0–500-m zone decreases rapidly with elevation (table 4). The 0–500-m zone is comparatively depauperate because it receives a species spillover only from above. The turnover from zone to zone increases significantly with elevation ($P < .05$; fig. 3). The latter pattern mainly reflects a significant increase in species' dropping out with increasing elevation rather than in replacement of one set of species by another. This is an expected result with the analogue trend in species richness per zone with elevation and when using Whittaker's beta index.

Maintenance of Species Richness: Stevens's Rapoport-Rescue Hypothesis

The narrow amplitude of climatic conditions with decreasing latitude is thought to be the ultimate cause of Rapoport's rule (i.e., latitudinal ranges of species become smaller with decreasing latitude; Stevens 1989). According to Stevens (1992), influential ranges of climatic variables decrease in similar ways on elevational and latitudinal gradients. Therefore, elevational ranges should increase with elevation (Rapoport's rule), and species richness should decrease monotonically with elevation (according to Stevens's Rapoport-rescue hypothesis) as they do with latitude. If they do not, "then the current explanation for the latitudinal Rapoport's rule and its potential influence on local species richness is somehow flawed" (Stevens 1992, p. 895). Rapoport's rule is not supported by Neotropical land birds, as species richness tends to form a hump-shaped pattern with elevation.

If Stevens's Rapoport-rescue hypothesis is correct, the frequency of species with sink habitats (sensu Shmida and Ellner 1984; see also Pulliam 1988) should be highest in the lowlands (Stevens 1992). This expectation is not supported by the analyses of turnover rates or the pattern of shared species between elevational zones (fig. 3; table 4). Midelevational zones have the highest number of species shared with other zones when compared with the 0–500-m zone and high-elevational zones. The species pools of these midelevational zones may thus comprise a larger share of species with marginal populations that may be poorly adapted to local conditions. At midelevations, it may thus be difficult for local core species to exclude marginal populations elevationally because of the proximity of core areas of these species in adjacent elevational zones (the rescue effect; Rosenzweig 1975; Brown and Kodric-Brown 1977; Shmida and Wilson 1985; Pulliam 1988). Such a hypothetical enhanced rescue effect in midelevational zones may be enforced by their central placement on the elevational gradient and the narrowness of the gradient.

While Stevens's Rapoport-rescue hypothesis could be relevant for the latitudinal gradient (Stevens 1989; but see Rohde et al. 1993; Colwell and Hurtt 1994; Roy et al. 1994; and references in these latter three), it does not seem to apply to the elevational gradient. The different conclusion reached by Stevens (1992)

is likely due to his focus on geographical ranges and dismissal of topographical features and geometric constraints—and perhaps sampling error—as being important (Colwell and Hurtt 1994).

Which Model Explains the Pattern?

The models discussed in this article are not 100% self-contained. The hump-shaped pattern seems to support a hump-shaped productivity model, but it could also be explained by an enhanced rescue effect at midelevation or by several other hypotheses not discussed in this article (for various alternative hypotheses, see, e.g., Lawton et al. 1987; McCoy 1990). However, the null model also predicts a hump-shaped pattern without any biological assumptions. In light of the quantitative results, the null model cannot be rejected as an adequate explanation, in spite of the skew in the curves. The biological models are potential hypotheses of mechanisms that may modify the pattern induced exclusively by the geometric constraints of the gradient, but they are not mutually exclusive.

The quest for single explanations for patterns has been described recently as unwise and unhelpful (Lawton 1996). I agree with this opinion and also believe that the search for a single explanation has delayed the progress in our understanding of what causes species richness to vary with elevation. The nonindependence of the various models discussed in this article ought to be obvious. For example, if productivity does indeed decline monotonically with elevation and the intermediate productivity hypothesis is correct, or if productivity has a mid-elevational peak and species richness is monotonically correlated with productivity, then the null model and the two productivity models predict, qualitatively, the same pattern, and they may act in concert to produce it.

Scale and Elevational Pattern of Tropical Birds

History, including local opportunities for speciation, often overrides the effects of equilibrium constraints and contributes to regional and local species richness (Ricklefs 1989). Important processes and their significance on local and regional patterns are unlikely to be the same (Rosenzweig 1975; Ricklefs 1987, 1989; Wiens 1989). It is possible that with more speciation events, more species can accumulate in an area, as life strategies of individual species can gradually be adapted to maintain the species at very low population levels. The latter can be true even within homogeneous rain forest habitats of the Amazonian lowland (Graves and Gotelli 1993). However, species that are sympatric or parapatric at a regional level may be allopatric on a finer scale (see also Stevens 1992; Graves and Gotelli 1993).

Most surveys on tropical birds conducted on a local scale seem to show a monotonic declining pattern of species richness with elevation (but see Rahbek 1995 for discussion). Although congeneric South American species on a regional scale tend to overlap altitudinally somewhere within their range, the exceptionally high number of species in the Andes may primarily be due to differentiation rather than an exceptionally high number of syntopic species on a local scale (Remsen 1985). The suggested dense vertical segregation of allied species

(Terborgh 1971, 1977), which should be regarded as a secondary state (Fjeldså 1994; see also Patton and Smith 1992; Arctander and Fjeldså 1994), could explain possible differences in the shape of regional and local elevational gradients of species richness.

Biomes versus Elevations

Division of the elevational gradients into arbitrarily defined elevational zones undoubtedly influences the perceived patterns of species richness. This is essentially an operational definition of scale, not a bias in itself. When working on a large regional scale, several distinctive biomes will be represented, each with its own level of species richness and unique species communities in the data. The number of biomes is likely to vary among elevational zones. Therefore, levels of biome heterogeneity are reflected by corresponding levels of species richness, and elevational peaks of species richness might tend to occur in the zones with the highest diversity of biomes.

How General Is the Elevational Pattern?

If the elevational gradient showed the same pattern across taxa, different from that of the null model (e.g., fig. 1D), we would expect the number of species to be related to some physical features (e.g., climate) that vary consistently with elevation. A comparison of available studies supports the generalization that species richness generally declines monotonically from mid- to high elevation on regional and also local scales (Rahbek 1995). In contrast, patterns of species richness below the median of complete gradients (i.e., from sea level to the mountaintop) vary considerably among taxa and geographical regions (based on an examination of the raw data reviewed in Rahbek 1995).

This variability is not surprising since only the geometric factor of potential primary-level mechanisms (*sensu* Pianka 1988) appears to be constant and independent of taxon, locality, and scale. Its influence, however, is likely altered by secondary mechanisms and may vary significantly among taxa because of differences in, for example, body size and population maintenance mechanisms (e.g., birds compared with small arthropods). Also, the ability to disperse elevationally is a potentially influential secondary factor because of the short elevational distances, and because climatic adaptations differ among taxa (e.g., bats vs. birds; see Graham 1990).

Furthermore, the patterns of speciation processes that influence the size of the available species pools across the elevational gradient differ among taxa but also within taxa among continents because of different geological histories (e.g., Ricklefs 1987, 1989; Latham and Ricklefs 1993). The spatial-temporal pattern of diversification during the upper Tertiary and Pliocene appears, for example, very different in South America and Africa (Fjeldså 1994).

There seems to be no reason to expect a globally uniform shape pattern in the precise shape of the elevational gradient of species richness, beyond the null model expectation of a midelevational peak.

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