The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevation plateau

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Herzog, S. K., Kessler, M. and Bach, K. 2005. The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. – Ecography 28: 209–222.

A monotonic decline in species richness with increasing elevation has often been considered a general pattern, but recent evidence suggests that the dominant pattern is hump-shaped with maximum richness occurring at some mid-elevation point. To analyse the relationship between species richness and elevation at a local scale we surveyed birds from lowlands to timberline in the Bolivian Andes. We divided the transect into 12 elevational belts of 250 m and standardized species richness in each belt with both individual- and sample-based rarefaction and richness estimation. The empirical data were then correlated to four explanatory variables: 1) area per elevational belt, 2) elevation (also representing ecosystem productivity), 3) a mid-domain effect (MDE) null model of geometrically constrained empirical range sizes, and 4) a hump-shaped model derived empirically for South American birds representing the regional species pool hypothesis. Local species richness peaked at ca 1000 m elevation, declined sharply to ca 1750 m, and then remained roughly constant. Elevation was the best single predictor, accounting for 78–85% of the variance in the empirical data. A multiple regression model with elevation, area, and MDE explained 85–90% of the variance. Monte Carlo simulations showed that the richness peak at 1000 m is the result of an overlap of two distinct avifaunas (lowland and highland) and that the correlation to MDE in the multiple regression was likely spurious. We recommend complementing correlation analyses involving MDE predictions with an examination of the distribution of range midpoints. The steep decline at mid-elevations was mainly due to a rapid loss of lowland species. The high-elevation plateau is striking and unexpected, but has also been found previously. It cannot be explained at present and exemplifies that despite several decades of research elevational gradients are still not well understood.

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The relationship between species richness and elevation has received considerable attention in the ecological literature. Equivalent to the latitudinal gradient in species richness, a monotonic decline in the number of species with increasing elevation has often been considered a general pattern (Brown and Gibson 1983, Begon et al. 1990, Rohde 1992, Stevens 1992).

However, Rahbek (1995) argued that this generalization is largely a result of too much emphasis on, and misinterpretation of, a few early studies (Terborgh 1977) combined with "citation inbreeding". In an extensive literature review including studies on a wide range of taxonomic groups, biomes, and spatial scales, Rahbek (1995) found empirical support for several

different elevational richness patterns, with a dominance of hump-shaped relationships where maximum species richness occurs at some mid-elevation point.

However, Rahbek (1995) also noted that most studies had methodological problems because they did not account for the effect of sampling effort and/or area on patterns of species richness. Failure to standardize data to account for sampling effort (Gotelli and Colwell 2001) and area (Rahbek 1995, 1997) can cause artefactual results. To overcome such pitfalls, Rahbek (1997) analysed a data set largely devoid of sampling biases on the elevational distribution of neotropical land birds. After controlling for the surface area of each elevational belt, the emerging regional-scale relationship between species richness and elevation was indeed hump-shaped with a maximum at ca 1000 m.

Stotz et al. (1996) approached the problem from a different angle. As not only surface area but also habitat diversity is greater in lowland Amazonia than on adjacent Andean slopes, Stotz et al. (1996: 37) only considered those species among lowland birds that inhabit terra firme forest and obtained a similar result as Rahbek (1997), namely a hump-shaped species-elevation curve with a maximum in the foothill zone between 500 and 1000 m. Thus, both analyses indicate that the enormous bird species richness of the Amazonian lowland is largely a consequence of its huge surface area and increased habitat diversity, and that if one controls for those factors, the lower Andean slope emerges as the zone of highest bird species richness.

Recent work on other groups of organisms also documented hump-shaped relationships between species richness and elevation, e.g. for trees in Costa Rica (Lieberman et al. 1996), for several plant groups in Bolivia (Kessler 2000c, 2001b), for ants in the western United States (Sanders 2002), and for non-volant small mammals in the Philippines (Heaney 2001), Malaysia (Md. Nor 2001), and Costa Rica (McCain 2004). However, several of those studies interpolated species presence between maximum and minimum observed elevations, which may cause an artificial hump in the species-elevation curve (Grytnes and Vetaas 2002). By contrast, Patterson et al. (1998) found a trough-shaped, but non-significant, relationship for murid rodents in Peru with richness maxima in the lowlands and in the highlands and a minimum at mid-elevations. For bats and birds, Patterson et al. (1998) reported a smooth, slightly curvilinear decline of richness with elevation, but their data were not standardized for area or habitat diversity. Patterson et al. (1998) remarked, however, that preliminary analyses of the same bird data set revealed a hump-shaped pattern once the effect of increased Amazonian habitat diversity was removed.

These studies seemingly illustrate that mountainsides do not simply mirror the latitudinal diversity gradient (Brown 2001) and that there is no universal agreement in the shape of the elevational pattern. Brown (2001) further argued that synthetic theories explaining the common patterns of species richness on elevational gradients have not been developed yet. Recent advances in null model theory, however, have added a new twist to an old story. Colwell and Hurtt (1994) proposed several models that simulate range size and randomise range placement within one-dimensional bounded geographical domains (e.g. an elevational gradient). Based entirely on stochastic processes these null models produce symmetrical curves with a mid-domain peak in species richness. These simulations are the ancestor of analytical null models (Willig and Lyons 1998, Lees et al. 1999, Jetz and Rahbek 2001) and analytical-stochastic null models (Colwell 2000, applied by Sanders 2002, McCain 2003, 2004) that have been tested against empirical data and extended to two-dimensional domains (Jetz and Rahbek 2001). These studies provide strong support for what has come to be called the mid-domain effect (MDE; Colwell and Lees 2000, Colwell et al. 2004).

By contrast, other authors (Bokma and Mönkkönen 2000, Koleff and Gaston 2001, Bokma et al. 2001, Hawkins and Diniz-Filho 2002, Diniz-Filho et al. 2002, Zapata et al. 2003) have dismissed a significant influence of MDE on spatial richness patterns, criticizing MDE model assumptions as unrealistic, conceptually flawed, or internally inconsistent. Colwell et al. (2004) contend that much of the MDE criticism is based on misunderstandings of the nature of null models and of MDE models in particular, the use of inappropriate frequency distributions of geographical range sizes, and an all-or-nothing approach searching for single-factor explanations. To properly evaluate the role of MDE in shaping species richness patterns Colwell et al. (2004) recommend that studies should a) quantitatively assess the relative importance of MDE instead of simply testing it as a null hypothesis, b) use re-sampling of the empirical range size frequency distribution (rather than theoretical range size frequency distributions or empirical range midpoints) for making MDE predictions, and c) apply multivariate analyses considering candidate explanations for richness patterns in addition to MDE. Of the 16 one-dimensional MDE studies found by Colwell et al. (2004) in an exhaustive literature review only one (McCain 2004) meets all three criteria.

In the present study, we follow the recommendations of Colwell et al. (2004) in analysing bird survey data from a perhumid elevational gradient from lowlands to timberline in central Bolivia. Lowland surveys were restricted to terra firme forest, and data analyses controlled for survey effort. Using multiple regression analysis we correlated the resulting pattern of species richness with the following explanatory variables: 1) area, 2) elevation (also representing potential evapotranspiration and mean canopy tree height), 3) MDE using the empirical version of the Colwell and Lees

(2000) constrained range-size null model, and 4) the regional species pool using Rahbek's (1997) hump-shaped model for South American birds.

Study area

We surveyed birds in and adjacent to Carrasco National Park on the east-Andean slope in the central Bolivian department of Cochabamba (Fig. 1). The area spans an elevational gradient from 200 to 4800 m. Its natural vegetation consists of evergreen, perhumid forest that once extended up to elevations of ca 4200 m. Due to centuries of human impact in the high Andes, the current timberline is lowered and generally found around 3400 m, but remnant forest patches remain at higher elevations (Kessler and Herzog 1998, Kessler 1999, 2000b). Foothill and lowland forests have been cleared extensively in recent decades, primarily for timber extraction, coca plantations, and road construction (Henkel 1995). Data on the vegetation of the study transect can be found in Ibisch (1996), Navarro (1997), and Kessler (2000a, 2001b).

We studied a continuous elevational gradient at 950–3400 m in the Serranía de Callejas (Fig. 1) using a ca 4-m wide gravel road abandoned in the 1980s. The adjacent forest was almost entirely in a natural state; few disturbed areas largely had reverted to montane forest, and the road partly had been invaded by woody plants. Human activity in the Serranía de Callejas increased drastically below 1000 m, and we collected data in two foothill area's. Between the villages of El Palmar and Villa Tunari (Fig. 1; 300–900 m) we selected several sites that contained some of the area's best-preserved primary or mature secondary forest. The second area at Río Ichoa-Cerro Leñe (Fig. 1; 300–750 m) contained pristine forest and was reached by helicopter. A seismic line (a straight trail just wide enough for one person) established several weeks before represented the only visible anthropogenic disturbance; no timber extraction or hunting had occurred. We surveyed lowland forest in the Valle del Sacta (Fig. 1; 220 m), a 5600-ha area of

primary and mature secondary terra firme forest. This area is separated from Andean forests by a ca 10-km wide belt of human settlements. It is located in the southernmost extension of Amazonian evergreen lowland forest, which forms a 10–30-km wide wedge at the base of the central Bolivian Andes. Further to the northeast evergreen forest is replaced by seasonally flooded savannah vegetation (Ribera et al. 1996).

Geologically, the bedrock mainly consists of sandstones, lutites, and quartzitic rocks of Devonian and Ordovician age (Montes de Oca 1997, Ergueta and Gómez 1997) with limited areas of granitic intrusives and calcareous rocks at 2000–2200 m along the study road and some white sand areas at 450–500 m. At Villa Tunari the geological substrate is composed of nutrient-poor white sandstones, whereas it consists of clayey red alluvial deposits in flat areas and more sandy soils on ridges in the Valle del Sacta.

Mean annual precipitation at the region's only reliable climatic station in Villa Tunari is 5676 mm (10 yr data; Ibisch 1996). Most precipitation falls from November to May, but even from June to October every month receives >100 mm. Ibisch (1996) estimated >3500 mm mean annual precipitation at 2200 m in the somewhat sheltered valley of Sehuencas (Fig. 1). Mid-elevation (1000–3000 m) slopes directly exposed to incoming clouds in the northwest of the park likely receive >8000 mm (Kessler 1999). Mean annual precipitation at Sacta is >3000 mm (Acebey pers. comm.), with additional moisture provided by frequent morning fog. Mean annual temperatures are 24.6°C at Villa Tunari and 12–15°C at 2200 m in Sehuencas (Ibisch 1996), with an annual variability of monthly means of ca 5°C. Nocturnal frosts occur down to 2000 m (Ibisch 1996, unpubl.), especially during periodic influxes of southern polar winds during the austral winter (Fjeldså et al. 1999).

Methods

Field surveys

We studied the continuous Serranía de Callejas transect (950–3400 m) from June to September 1996 and sections of it (950–1500 m, 3000–3400 m) again in October 1997. The El Palmar-Villa Tunari area (300–900 m) and the Valle del Sacta (220 m) were studied in September and October 1996, and Río Ichoa-Cerro Leñe (300–750 m) in September 1997. No surveys were conducted above timberline (3400 m). To factor out the effect of increased lowland habitat diversity on species richness, lowland field work was restricted to terra firme forest.

The survey method is detailed in Herzog et al. (2002) and only briefly summarized here. While walking slowly and quietly from dawn to mid-day and often again from late afternoon to after dusk along roads, trails and
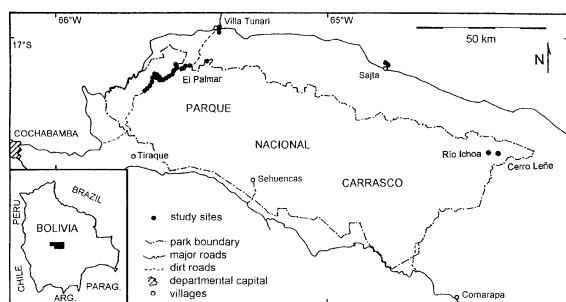

Fig. 1. Location of Carrasco National Park in Bolivia and distribution of survey sites within the study area.

through the habitat where feasible, SKH continuously recorded all visual and acoustical observations of birds (including numbers of individuals per species) within 50 m of the observer. The observer's movement rate largely depended on the level of bird activity. When spending longer periods in one spot and during very occasional re-sampling of an area (the latter occurred to approximately the same degree in all elevational belts and thus did not introduce a systematic error), repeated counts of obviously territorial individuals were avoided. Tape recordings were made extensively to supplement obser-vations and to identify unknown voices, and were integrated into the master list of temporally consecutive observations. Fjeldså (1999) quantitatively compared this approach with standardized point counts. Its main advantages compared to any timed species-count method (e.g. point counts) are time efficiency and relative observer independence (Fjeldså 1999, Herzog et al. 2002).

Transect subdivision

We divided the transect into 14 elevational belts of 250 m (<250 m, 250–499 m, 500–749 m, etc.; Table 1). We restricted surveys to forest areas, but included data from small areas of natural (e.g. landslides) or anthro-pogenic (e.g. small coca fields) disturbance. Species occurring naturally at forest edge were included in all analyses; species depending on aquatic habitats were excluded.

For analysing the relationship between species rich-ness and elevation, data from the El Palmar-Villa Tunari area were excluded for two reasons (but they were included in the analysis of range midpoints). First, human disturbance probably introduced biases that we were unable to control for. Second, individual survey sites with suitable habitat were spaced relatively far apart and measured species richness included a strong com-ponent of beta diversity (sensu Whittaker 1972), rather than alpha diversity as on the remaining transect. Thus, the Río Ichoa-Cerro Leñe data were used for the 300–499-m and 500–749-m belts, and no data were available for the 750–999-m belt. Although surveys extended to 3400 m, the accessible area in the 3250–3499-m belt was too small for meaningful data analysis and it was excluded. For the Serranía de Callejas only data collected in 1996 were used in this step of the analysis.

Due to topographic complexity and variations in the amount of accessible habitat, it was not feasible to standardize survey area across all elevational belts. Survey distance (length of transect line) varied from 3.9 km (2750–2999 m) to 10.3 km (300–499 m) with a mean of 5.6 km.

Table 1. Observed and estimated species richness values of elevational belts studied along the Carrasco transect on the east Andean slope in central Bolivia. Only those belts included in the analysis of the relationship between species richness and elevation are shown. Elevation in m.

	220	300-499	500–749	1000–1249	1250–1499	1500–1749	1750–1999	2000–2249	2250–2499	2500–2749	2750–2999	3000–3249
Lists[a]	45	80	27	51	56	49	20	36	20	21	20	20
Individuals per list[b]	12.6±2.7	14.7±14.0	12.5±1.9	14.1±3.2	14.7±3.9	15.6±4.9	16.9±6.9	17.6±6.4	20.5±8.2	19.9±6.5	18.5±6.8	18.5±6.0
Total individuals	569	1175	337	719	821	765	337	633	409	417	369	369
S_{obs}^c	119	141	100	133	110	106	63	76	58	57	61	56
Sample-based rarefaction												
MMMean max[d]	153	161	149	174	132	129	84	88	76	71	82	72
MMMean std[e]	141	136	149	158	119	120	79	71	66	60	78	68
Individual-based rarefaction												
S_{obs} std[f]	98	96	100	103	85	82	63	62	55	53	59	55
MMMean max[g]	146	156	139	162	125	121	74	82	64	61	70	65
MMMean std[h]	137	132	139	146	111	109	74	73	62	58	69	64

[a]Number of 10-species lists (samples) compiled.
[b]Mean number of individuals per 10-species list (sample)±SD.
[c]Observed total species richness.
[d]MMMean estimate of species richness after the maximum number of samples.
[e]Sample-based MMMean estimate of species richness standardized for survey effort.
[f]Observed species richness after 337 individuals.
[g]Individual-based MMMean estimate after maximum number of individuals.
[h]Individual-based MMMean estimate after 337 individuals.

Standardisation of survey effort for species richness estimation

Survey effort was not exhaustive and varied between elevational belts, precluding the use of raw species counts in our analyses. Therefore, we used three methods to standardize species richness values for survey effort (Table 1).

First, we used a modified version of the "m-species-list method" (MacKinnon and Phillipps 1993, Poulsen et al. 1997) following the recommendations of Herzog et al. (2002) (method 1). We divided the master list of temporally consecutive bird observations in each 250-m belt into lists of 10 species: the first list consists of the first 10 species observed, the second list includes the following 10 species and may contain species already found on the first list, and so on. We then plotted cumulative species number as a function of list number, treating each 10-species list as a separate sample. By randomising sample accumulation order 50 times using EstimateS 5.0.1 (Colwell 1997), we obtained sample-based rarefaction curves and estimated total species richness in each belt with the MMMean statistic (Fig. 2; Raaijmakers 1987, Keating and Quinn 1998). For species-rich neotropical bird data sets, MMMean was the least biased of nine estimators evaluated by Herzog et al. (2002), but a drawback of MMMean is that no statistically sensible variance estimator exists (Colwell and Coddington 1994, Colwell pers. comm.). Ideally, the MMMean curve for each elevational belt would quickly reach an asymptote after 10–15 lists. As this was not the case, we standardized all data sets for survey effort following the procedure in Herzog et al. (2002) (Fig. 2).

Gotelli and Colwell (2001) suggested that x-axes of sample-based rarefaction curves should be rescaled from samples to individuals because datasets may differ systematically in the number of individuals per sample. Thus, our second standardisation method (method 2) is derived from individual-based rarefaction. Accumulation order of individuals was randomised 50 times using EstimateS 5.0.1 (Colwell 1997), and we used the observed species richness after 337 individuals (the lowest number of individuals recorded in any elevational belt; Table 1) as the standardized cut-off point. In the third method, we determined MMMean values of estimated species richness after 337 individuals from the same individual-based rarefaction curves using EstimateS 5.0.1 (Colwell 1997) (method 3).

Individual-based rarefaction probably is the least biased method for comparing species richness via species-accumulation curves (Gotelli and Colwell 2001), but it is not without problems. In cases with strongly differing sampling intensities, such as here (Table 1), it implies a loss of much valuable data. It also is sensitive to biases in the quantification of the number of individuals per species. Such biases are
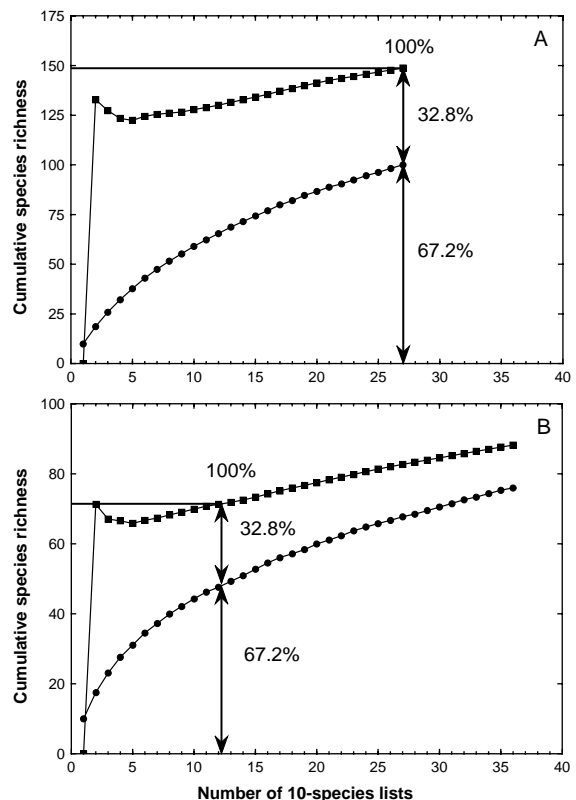

Fig. 2. Sample-based rarefaction curves for bird data sets from two elevational belts (A: 500–749 m; B: 2000–2249 m) in Carrasco National Park, Bolivia. Observed (S_{obs}; circles) and estimated species richness using the MMMean statistic (squares) are expressed as a function of the number of 10-species lists. Sample accumulation order of all curves was randomized 50 times, and each point represents the mean of the resulting 50 values. To control for the confounding effects of survey effort, we determined a standardized cut-off point from the relation between the S_{obs} and the MMMean curve: for each data set, every S_{obs} value was expressed as the proportion of the respective MMMean value (Herzog et al. 2002). Survey effort was lowest in the 500–749-m belt (A), where S_{obs} comprised 67.2% of the estimated richness (149 species) at maximum sample size (27 10-species lists). The equivalent cut-off point was determined for all other data sets as illustrated for the 2000–2249-m belt (B), where a standardized estimate of 71 species was obtained.

inevitable when studying birds in tropical forests, where many birds are only seen briefly and where many species move in large mixed-species flocks. Also, the presence (or absence) of a few large single-species flocks of some species, e.g. swifts or parrots, can strongly influence total individual numbers and thereby the slope of the accumulation curve, artificially inflating survey effort. Finally, whereas species richness values obtained by individual-based rarefaction may accurately reflect relative differences in species richness between sites, they almost invariably underestimate true species richness and usually are lower than the total observed species numbers.

Species richness estimation based on samples such as m-species lists is less sensitive to these problems by including all or most of the collected data, by counting a species only once when two or more individuals are registered together, and by providing species richness values somewhat above the observed values. However, this method also has three important weaknesses (Gotelli and Colwell 2001). First, different estimation methods provide different results, and although there is some empirical data to suggest which statistic might be suitable for a given data set, no general test exists to choose the least biased estimator (of course this also applies to individual-based richness estimation). In general, the response of estimators to differences in species abundance distributions, species richness, etc. is poorly understood. Second, the mean number of individuals per list tends to be higher in species-poor habitats, simply because more birds have to be recorded to accumulate 10 (or five, or 20) species. This leads to relatively steeper accumulation curves in species-poor habitats, and hence an overestimation of species richness relative to species-rich habitats. Finally, and perhaps most importantly, the arbitrary decision on how many species to include in each list will influence the estimated values. High species numbers per list will reduce the number of lists and lead to relatively steeper accumulation curves and higher estimates (Herzog et al. 2002). All three error sources will be stronger in cases with more pronounced differences in actual species richness between sites.

Given the potential biases of both approaches for obtaining comparable, standardised species richness values, here we chose to apply both sample- and individual-based rarefaction. As the elevational richness patterns obtained by both approaches are highly correlated (Spearman rank correlation, values of standardization method 1 vs method 2: $r = 0.98$, $p < 0.0001$; method 1 vs 3: $r = 0.99$, $p < 0.0001$; method 2 vs 3: $r = 1.00$, $p = 0$), we conclude that our raw data are fairly robust to standardization, and that both standardization approaches accurately reflect the richness pattern captured by our field data. On the other hand, since the raw species counts show lower correlation values with the standardized data (Spearman rank correlation, raw data vs method 1: $r = 0.85$; raw data vs method 2: $r = 0.88$; raw data vs method 3: $r = 0.87$; $p < 0.001$ in all cases), we conclude that standardization is appropriate.

Explanatory variables

Area – due to the conical shape of mountains, land surface area decreases steadily with increasing elevation (Graves 1988, Rahbek 1997). The effect of the area of elevational belts on species richness at the regional scale was illustrated by Rahbek (1997), but the procedures used therein to control for area are not applicable to our local-scale data set. Rahbek (1997) also used belts of greater amplitudes than analysed here. As a proxy for area we measured the horizontal width of each 250-m belt in central Bolivia on topographic maps (scale 1:50 000) issued by the Inst. Geográfico Militar, La Paz, Bolivia. For the lowland belt we measured only the area covered by evergreen terra firme forest as surveys were restricted to this habitat, excluding open savannah further east. We took five measurements for each belt (one in the study area, two to the north, and two to the south at 10 km intervals), and the mean was calculated and rounded to the closest 100 m (Table 2). As species richness does not increase linearly with area, we multiplied the mean horizontal width of each belt by an area-dependent factor, assuming a slope of $z = 0.13$ in a double-log species-area plot, which corresponds to the mean z value obtained for birds in the tropical Andes by Rahbek (1997: Fig. 2c).

Elevation – this represents the model of a monotonic decline of species richness with elevation (Stevens 1992). We used the mean elevation of each belt, except for the lowland belt, where we used the actual elevation (Table 2).

Ecosystem productivity – Kessler (2001b) determined potential evapotranspiration (PET) calculated after Thornthwaite and Mather (1957) and mean canopy tree height in mature forest as indices of ecosystem productivity (Rosenzweig 1968, Lieth 1975) for our study area. Within the boundaries of the present gradient, both PET (Pearson correlation: $r^2 = 1.00$, $p = 0$) and mean canopy tree height (Pearson correlation: $r^2 = 0.95$, $p < 0.0001$) closely correlate negatively with elevation. Hence, only elevation is used in the regression analysis.

MDE – we used the richness values predicted by the empirical version of the Colwell and Lees (2000: Box 5) constrained range-size null model, shuffling empirical range size distributions by random mid-point Monte Carlo simulations using RangeModel 3.1 (Colwell 2000: Model 4). Upper and lower domain limits were defined as the natural upper limit of humid forest on the eastern slope of the central Andes (ca 4200 m) and the lower limit of Amazonian evergreen forest (sea level), respectively. Only those species whose elevational distribution throughout the neotropics falls entirely within these domain limits were included in the model. Upper and lower elevational range limits were taken from standard references on neotropical birds (Ridgely and Tudor 1989, 1994, Fjeldså and Krabbe 1990, Hoyo et al. 1992–2002, Stotz et al. 1996, Isler and Isler 1999, Ridgely and Greenfield 2001, Hennessey et al. 2003). Unlike Lees et al. (1999), who defined their domain as the present day extent of forest cover on Madagascar, we did not use the present elevation of the closed upper timberline (ca 3400 m) as the upper domain limit because remnant forest patches of varying sizes still

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Table 2. Values of the explanatory variables for each elevational belt included in the analysis of the relationship between species richness and elevation. Elevation in m.

	220	300–499	500–749	1000–1294	1250–1499	1500–1749	1750–1999	2000–2249	2250–2499	2500–2749	2750–2999	3000–3249
Area[a]	15.0	3.0	1.6	0.8	0.7	0.7	0.6	0.6	0.5	0.5	0.5	0.4
Elevation[b]	220	400	625	1125	1375	1625	1875	2125	2375	2625	2875	3125
MDE[c]	70	116	174	288	334	364	384	387	376	353	318	268
Species pool[e]	589	630	662	682	666	638	606	561	512	463	407	351

[a] Horizontal width in km determined from topographical maps (mean of five measurements rounded to the closest decimal).
[b] Mean elevation of each belt, representing both elevation per se as well as PET and mean canopy tree height as indices of ecosystem productivity.
[c] Values predicted by the empirical version of the Colwell and Lees (2000: Box 5) and Colwell (2000: Model 4) constrained range-size MDE null model for 548 species.
[e] Values predicted by Rahbek's (1997) regional hump-shaped model for South American birds.

exist up to elevations of 4200 m in the study area, in part only a few kilometers from our actual study sites (see, e.g. photos in Kessler 2000b). While these patches were not accessible to us, they certainly provide suitable habitat for the local forest-based avifauna, and the upper elevational distribution of the bird species is consequently not limited to the forest line at 3400 m along the study road.

Extensive ornithological surveys in Carrasco National Park and adjacent lowland forests in recent years by a number of field workers (especially R. MacLeod, J. Fjeldså, and collaborators) have resulted in a nearly complete inventory of the area's avifauna (Herzog et al. unpubl.). With the exception of species depending primarily on aquatic habitats and lowland species not found in terra firme forest, all recorded species that inhabit humid forest were included in the null model computations. An additional 19 species that have gone unrecorded so far but that are expected to occur in the area also were included, resulting in a total of 548 species. Monte Carlo simulations were replicated 20 times and mean richness values were computed for 60 domain divisions (the default of RangeModel 3.1). Predicted values for each 250-m belt were taken from the resulting curve (Table 2).

As some of the MDE debate has focused on whether to use theoretical or empirical range size frequency distributions for MDE predictions (Colwell et al. 2004), we also computed the bivariate uniform model of Colwell and Lees (2000: Box 2), which is equivalent to the Colwell and Hurtt (1994) null model 2 of bounded random geographical ranges, for 548 species using RangeModel 3.1 (Colwell 2000: Model 1). This theoretical model takes no account of the empirical range size frequency distribution. As above, Monte Carlo simulations were replicated 20 times and mean richness values were computed for 60 domain divisions. As both null models were highly correlated (Pearson correlation: $r^2 = 0.99$, $p < 0.0001$; however, the constrained range size model predicted higher absolute values than the bivariate uniform model) only the constrained range size model is used in the analysis.

Regional species pool – the regional species pool has been proposed as a significant determinant of local species richness as it places an upper limit on the number of species potentially able to colonise local habitats (Cornell and Lawton 1992, Caley and Schluter 1997). We considered Rahbek's (1997) regional hump-shaped model for South American birds as the most appropriate regional source pool model and used the richness values predicted by this model (Fig. 4 in Rahbek 1997; values taken from the fitted curve) for each of our elevational belts (Table 2). It may be argued that this model is incorrect to some degree as it is based on partly interpolated species-distribution data (see Grytnes and Vetaas 2002). However, at the broad spatial scale

considered by Rahbek (1997) we regard the data on South American bird distributions as sufficiently complete so as to render the influence of interpolation on the species-elevation curve negligible.

Multiple regression analysis

We first performed bivariate linear regressions of the empirical species richness pattern (separately for each of the three standardization methods) against each of the four explanatory variables individually, followed by multiple regression analysis. Due to the spatial proximity of most elevational belts, estimates of species richness violate statistical assumptions of independence, and the present analysis therefore focuses on the proportion of variance explained rather than on probability values. All regression and correlation analyses were performed using STATISTICA for Windows (ver. 5.1, Anon. 1997).

Monte Carlo simulations: range midpoints and turnover

To asses whether species are randomly distributed along the elevational gradient or show clear zonations, we conducted Monte Carlo simulations with a program written by KB in Visual Basic within EXCEL. Observed elevational ranges of all recorded species were randomly placed along the elevational gradient treating the gradient's end points as hard boundaries not to be crossed by any species' range. Total species number per belt was constrained in two ways, according to the MMMean-standardized observed richness pattern, and to the richness pattern predicted by the MDE constrained range size model. Early simulation trials showed that not all species could be accommodated in the simulations using the observed standardized species richness. This was a result of tight species packing in the empirical data, whereas in the randomised data many gaps between species could not be filled because they were narrower than the species ranges remaining to be placed. Therefore, the observed standardized data was multiplied by the factor 1.5. The MDE model values were high enough that this correction was not necessary. Randomisations were repeated 1000 times, and we calculated the mean and 95% confidence intervals for three parameters (midpoints per belt, number of upper/lower elevational limits per belt, species turnover between adjacent belts) explained below. These values were compared to the observed data, assuming that empirical and predicted values were significantly different if the observed value fell outside the 95% confidence intervals of the predicted value.

Midpoints: as hump-shaped patterns that may correlate to MDE predictions can arise from a variety of different processes, we compared not only the observed and predicted species richness patterns but also the empirical and predicted range midpoint distributions, counting the number of midpoints per belt (Grytnes 2003).

Upper and lower limits: to asses whether species turnover along the gradient is homogeneous, we separately compared the number of upper and lower elevational limits per belt of empirical vs simulated data.

Turnover: as a further test for species zonation, species turnover along the gradient was measured with the Wilson-Shmida index (Wilson and Shmida 1984). The index is calculated for pairs of adjacent elevational belts as follows:

$$\beta = (b + c)/(2a + b + c)$$

where a is the number of species recorded in both belts, and b and c the number of species lost and gained, respectively. The more dissimilar two belts are, the higher is the index, reaching a maximum of 1 at total dissimilarity. The Wilson-Shmida index produces results comparable to those of other β-diversity indices (Davis et al. 1999, Koleff et al. 2003).

Results

We recorded a total of 449 bird species, 38 of which were found only in the El Palmar-Villa Tunari area. Species richness peaked around 1000 m and slightly decreased towards the lowlands (Fig. 3, Table 1). Above 1250 m species richness decreased quickly to a minimum at 2500 m, followed by a slight increase towards the highest elevation. In general, however, variation above 1750 m was slight and richness remained surprisingly constant, generating a high-elevation plateau (Fig. 3, Table 1).

Examining the congruence between empirical and model data (Fig. 3, Table 3), elevation (also representing ecosystem productivity) was the best predictor variable explaining 78–85% of the variance in the empirical species richness pattern. The regional species pool was a moderate predictor of the empirical pattern, explaining 59–63% of its variance. At low elevations it was largely in accordance with the empirical curve, but above 1250 m observed species richness decreased much faster than predicted by this model (Fig. 3D). Area had little explanatory power, concurring with the empirical pattern only in the lowlands (Fig. 3A). MDE predictions were negatively correlated to and strongly contrasted with the observed species richness pattern. The former reached its peak at elevations where the latter approached its minimum (Fig. 3C), and the maximum richness predicted by the MDE model is over twice as high as the empirical richness peak (Table 1).

The best multiple regression model was elevation combined with area and MDE, explaining 85–90% of

Fig. 3. Comparison of the empirical richness pattern (circles; standardized for survey effort by MMMean estimates for samples) and the patterns predicted by the four explanatory models examined (squares): (A) area, (B) elevation, (C) mid-domain effect, and (D) regional species pool. Empirical data were not standardized for area since area was included as an explanatory model. Curves were fitted by distance-weighted least-squares smoothing.
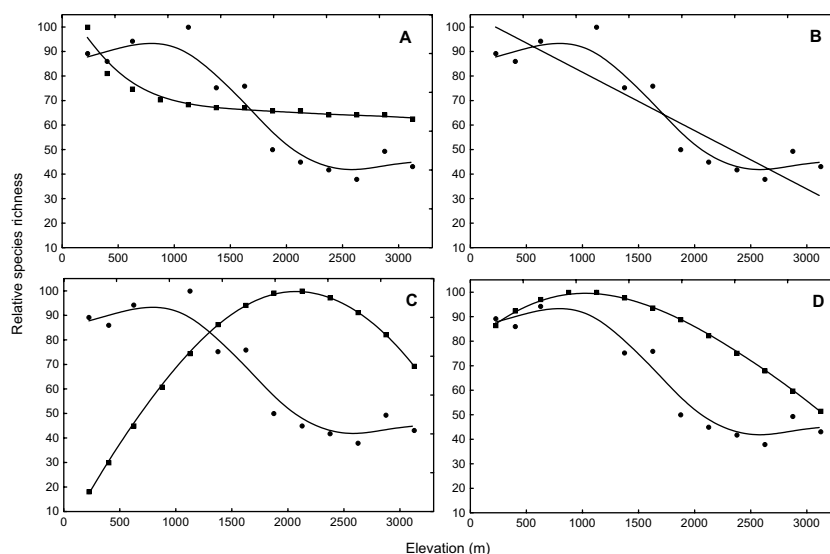
the variance in the empirical species richness pattern (Table 3). The multiple regression of richness vs. regional species pool and area combined also obtained high determination coefficients of 0.72–0.79 (Table 3).

The proportion of observed range midpoints was significantly higher at 250–750 m and 3000–3250 m than predicted by the Monte Carlo simulations (Fig. 4). Thus, the empirical richness peak at ca 1000 m results at least partly from a large number of species restricted to low elevations. The significant surplus of elevational midpoints at 3000–3250 m might be a sampling artefact as species mainly occurring at higher elevation and barely entering our study gradient, are falsely considered as having their mid-points in the highest survey belt.

Further, the results of the analyses of range midpoints may be biased by two shortcomings in our data set, i.e. the sampling gap at 750–999 m and the fact that the area from 300 to 750 m was surveyed in a separate location. Both shortcomings may potentially inflate the number of midpoints at elevations of 300–750 m because species actually reaching up to 750–999 m may be misinterpreted as having their upper elevational limits at lower elevations, and because species found only at the separate survey location could not be recorded above 750 m. However, we doubt that these potential biases are a major problem, for two reasons. First, the survey data from the El Palmar-Villa Tunari area were included in determining the elevational ranges of species. As a result,

Table 3. Linear determination coefficients (r^2) between observed species richness standardized by three methods and four explanatory model response variables. The upper four lines show the individual regression values, the lower six lines multiple regressions combining two and three parameters (starting with elevation as a fixed variable because it has the highest single explanatory power). Since Rahbek's (1997) regional species pool model is corrected for area, we also performed a multiple regression combing species pool and area. Note the consistency in results between the three richness estimation methods.

	Sample-based standardized MMMean estimate	S_{obs} after 337 individuals	Individual-based standardized MMMean estimate
Area[a]	0.37	0.43	0.43
Elevation (E)[b]	0.78	0.85	0.84
MDE[c]	0.43	0.46	0.47
Species pool[e]	0.59	0.63	0.60
E and area	0.81	0.87	0.85
E and MDE	0.78	0.85	0.84
E and species pool	0.79	0.86	0.84
E and area and MDE	0.85	0.90	0.88
E and area and species pool	0.82	0.88	0.86
Species pool and area	0.72	0.79	0.77

[a]Horizontal width in km determined from topographical maps (mean of five measurements rounded to the closest decimal).
[b]Mean elevation of each belt, representing both elevation per se as well as PET and mean canopy tree height as indices of ecosystem productivity.
[c]Empirical version of the Colwell and Lees (2000: Box 5) and Colwell (2000: Model 4) constrained range-size MDE null model for 548 species.
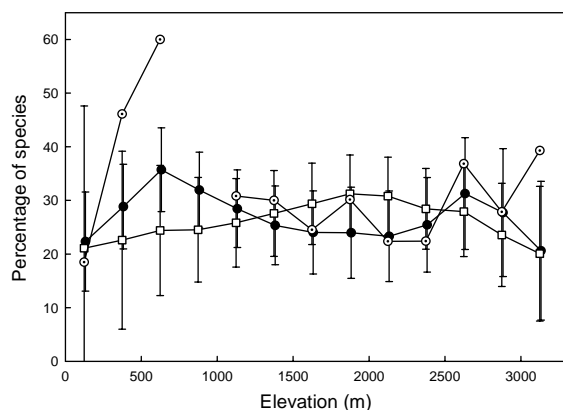[e]Rahbek's (1997) regional hump-shaped model for South American birds.

Fig. 4. Proportion of empirical range midpoints (open circles) and those predicted by Monte Carlo simulations restricting species richness per elevational belt according to the empirical richness pattern (closed circles) and MDE model predictions (squares). Vertical bars indicate 95% confidence intervals of the predicted values based on 1000 randomizations.

empirical range midpoints are affected only by an elevational gap of 50 m (900–950 m), and it is unlikely that such a negligible a gap will inflate the number of range midpoints below it. Second, with regard to the separate location of the area from 300 to 750 m, of the 127 species that had their midpoints within this elevational range only 16 (13%) were exclusive to that area. For these 16 species, the mean upper elevational limit in Bolivia (based on Hennessey et al. 2003) is 1440 m. This implies that their elevational midpoints would be located at ca 700 m elevation. As a result, even if surveys at the separate site had extended to higher elevation and recorded the full elevational ranges of these species, their range midpoints would still be located well below the elevation predicted by the MDE model.

Regarding species zonation, significantly more lower limits than expected by chance occurred at 220–500 m, 1000–1250 m, and 3000–3250 m, and significantly fewer lower limits at 500–750 m (Fig. 5A). Upper elevational limits showed significantly higher values at 500–750 and 1500–1750 m and significantly lower values at 250–500 m, 1750–2000 m, and above 2500 m (Fig. 5B). Turnover was significantly higher than expected from the Monte Carlo simulations at 750–1250, 1750 and 2500 m, and lower at 200–500, 2000, and 3000 m (Fig. 6). Taken together, these analyses show that the change of species composition along the elevational gradient is not smooth. Rather, areas of rapid change and others of limited turnover exist. However, the location of peaks of upper and lower elevational species limits and of peaks in species turnover are not concordant and it is difficult to point out distinct elevational zones.
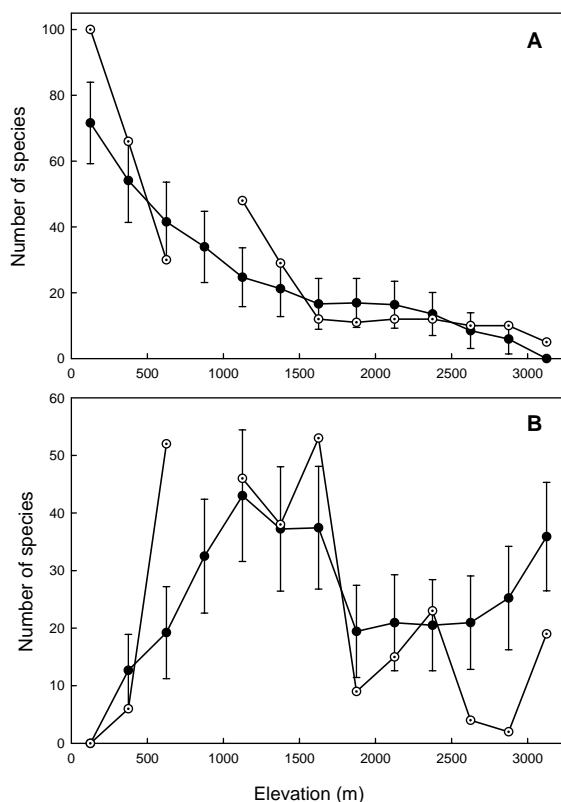

Fig. 5. Number of lower (A) and upper (B) elevational range limits observed (open circles) and predicted by Monte Carlo simulations restricting species richness per elevational belt according to the empirical richness pattern (closed circles). Vertical bars indicate 95% confidence intervals of the predicted values based on 1000 randomizations.

Discussion

The elevational pattern of bird species richness at the local scale documented here shows three distinct zones: a slight increase from the lowlands to a maximum at ca 1000 m, a sharp decline at 1250–1750 m, and roughly constant values up to the highest survey elevation at 3250 m. Of course, at even higher elevations at and above timberline species richness will decrease. Among the four models examined, this pattern best fits the elevation model, although there are noticeable discrepancies. Neither the slightly lower values in the lowlands, nor the sharp decline at mid-elevations, nor the richness plateau at high elevations are adequately predicted by this model. In the multiple regression model, these divergences are partly accounted for by the additional factors included. Area predicts fairly constant and high values at higher elevations, thus modelling the high-elevation plateau. The MDE model, by contrast, predicts a mid-elevation peak and, although negatively correlated with the observed pattern when compared directly, in the multiple regression model, it explains the
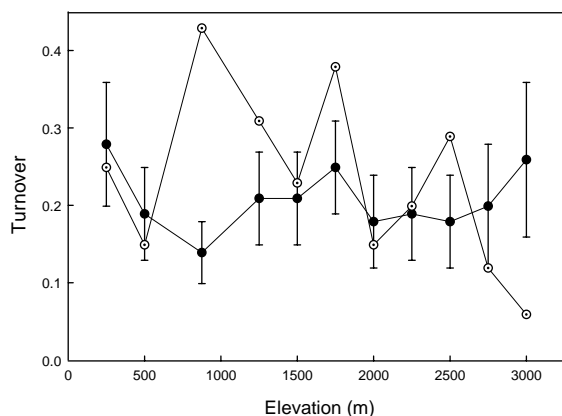
Fig. 6. Species turnover between adjacent elevational belts calculated with the Wilson-Shmida index (Wilson and Shmida 1984) for the empirical data (open circles) and predicted by Monte Carlo simulations restricting species richness per elevational belt according to the empirical richness pattern (closed circles). Vertical bars indicate 95% confidence intervals of the predicted values based on 1000 randomizations.

peak in the foothills and the decrease of species richness towards the lowlands.

The rather good correlation between the observed richness pattern and elevation indicates that local ecosystem properties may be involved in shaping the pattern. However, for two reasons we are unable to pinpoint which local factors might be responsible. First, most local factors co-vary closely along the gradient and cannot be disentangled. Potential evapotranspiration and canopy height decline almost linearly with elevation (see Methods). Other factors not quantified by us, e.g. insect abundance and habitat complexity, very likely decline in a similar fashion with elevation. Which of these factors or factor combinations are ultimately the most important can only be determined by comparing different transects where these variables show different distributions. Second, there is no consensus about the general relationship between richness and productivity. Both monotonic and hump-shaped relationships have been documented (Waide et al. 1999, Mittelbach et al. 2001). As yet, no comprehensive theoretical framework exists for the mechanisms involved in productivity-richness relationships (Currie et al. 1999, Ricklefs 2004).

Regardless of the causes for the correlation between the empirical pattern and elevation, we are still faced with explaining the three deviations outlined above, i.e. the foothill hump, the sharp mid-elevation decline, and the high-elevation plateau. Among the models considered here, the foothill peak is best predicted by the regional species pool model. Rahbek (1997) concluded that the regional skewed mid-elevation peak is best explained by geometric boundary constraints, i.e. MDE, whereas the details of the pattern are governed by other factors. However, our Monte Carlo simulations suggest that the contribution of MDE to the multiple

regression model is likely spurious. If this model were to explain the foothill richness peak, we would also expect a peak of elevational midpoints at the same elevation. This simply is the result of the nature of the mid-domain null model. Species are randomly placed along the gradient, accumulating at mid-elevations because species with large elevational amplitudes must occur in the middle of the gradient (Colwell and Lees 2000, Colwell et al. 2004). As shown by Laurie and Silander (2002), Grytnes (2003), and our simulations (Fig. 4), this leads to a slight mid-domain peak of range midpoints. By contrast, in our empirical data midpoints are accumulated at low elevations. In combination with the zonation simulations (Figs 5 and 6), this can be interpreted as reflecting a prominent low-elevation avifauna. This avifauna can be detected by the high number of lower elevational limits at 220–500 m, the surplus of midpoints at 250–750 m, and the high number of upper elevational limits at 500–1250 m. Thus, the peak of species richness at 1000 m apparently results from an overlap of a distinct lowland with a distinct highland avifauna, and coincides with the significant peak of species turnover at 750–1250 m. When assigning all recorded species to mutually exclusive categories of lowland species (present below 300 m) and highland species restricted to elevations above 300 m, this overlap and richness accumulation becomes apparent (Fig. 7). Although this seems trivial at first sight, there is no a priori reason to assume that the overlap between the two regional species pools leads to a hump-shaped richness distribution. It is equally conceivable that the decline of lowland species is sufficiently strong and/or the increase of highland species so weak that the resulting overall richness curve peaks in the lowlands.

The sharp decline of species richness at 1250–1750 m is largely caused by the rapid loss of lowland species. This decline is evidenced in the large number of upper elevational limits at this elevation (Fig. 5B) and causes high species turnover at 1750 m (Fig. 6). The high-elevation plateau at 1750–3250 m is puzzling, although we are not the first to document this pattern. Local bird species richness in Manu National Park of south-central Peru (Patterson et al. 1998: Fig. 1a) shows a similar plateau with almost identical richness values, but this phenomenon is not discussed. For geometrid moths in southeast Ecuador, Brehm et al. (2003) also found roughly constant values at 1800–2700 m. A high-elevation richness plateau is not predicted by Rahbek's (1997) hump-shaped model or by the geometric null model, and strongly disagrees with the productivity hypothesis. Currently we have no plausible explanation for it. Although area apparently accounts for the plateau to a certain degree in our multiple regression model, we cannot conceive any causal relationship.

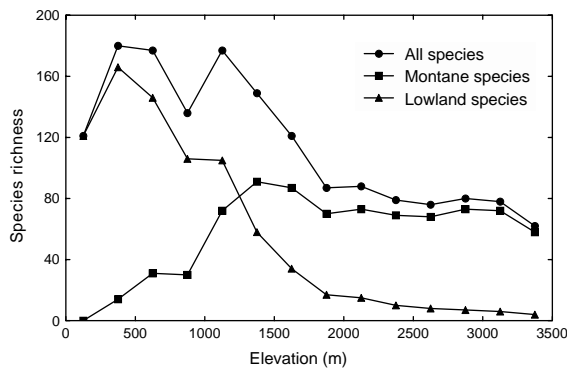Comparing our results with those of other avian transect studies in the Neotropics, we find substantial

Fig. 7. Changes in species composition along an elevational gradient on the east Andean slope in central Bolivia. Montane species were defined as restricted to areas above 300 m and absent from the lowlands, whereas lowland species may or may not occur in montane areas. Elevational ranges of species were interpolated to all elevations between the recorded minimum and maximum of each species. Since interpolation added no species to the lowest and highest elevational belt, values for these belts are negatively biased, whereas a sampling bias accounts for the minimum at 750–999 m. Note the nearly constant number of montane species between 1750 and 3250 m.

similarities. When removing the effect of increased lowland habitat diversity from their Manu data set, Patterson et al. (1998) found that species richness peaked around 1000 m rather than in the lowlands, i.e. exactly at the same elevation as in our study. Stotz et al. (1996: Fig. 3.3) reported similar cases. Whereas absolute richness values of these studies and ours coincide above about 2000 m, our values are much lower on the remainder of the transect. The avifauna of lowland terra firme forest in our study area is depauperate due to its semi-isolated location at the end of a narrow (10–30-km wide), ca 500-km long band of lowland forest wedged in between the Andes and open savannah habitats. Consequently, many bird species typical of Amazonian forest are lacking despite ecological conditions that in principle appear suitable. Blake and Loiselle (2000) found a diversity peak at 500 m in Costa Rica based on mist net captures, but point count data from the same transect indicated highest richness at 50 m. Although Blake and Loiselle (2000) standardized their data for sampling effort, they did not account for the effect of area. A reanalysis controlling for area seems worthwhile and we suspect that a hump-shaped pattern would result regardless of the survey method. Terborgh (1977: Fig. 5) also found a richness maximum at mid-elevation in Peru when controlling his data for sampling effort, but as noted by Rahbek (1995), only Terborgh's non-standardized graph depicting a monotonic decline of species richness is usually cited even in recent papers (Heaney 2001). In conclusion, when excluding birds of seasonally flooded forests, a maximum of bird species richness in the foothills appears to be a general pattern in the Neotropics.

Taking into account other taxonomic groups along the same gradient can be an effective way to determine general species richness patterns (Heaney 2001). Two other groups of organisms have been studied in Carrasco at largely the same sites as birds. Köhler (2000) surveyed amphibians at 500–2500 m, and species richness peaked at 1500 m. However, amphibian species richness is about four to five times higher in adjacent lowland forests than at 1500 m (Köhler and Reichle pers. comm.). This probably reflects the influence of temperature on the diversity of ectothermic organisms and the absence of lentic waters in montane forests required for the reproduction of many amphibians (Köhler 2000). By contrast, alpha diversity of most of the six plant groups sampled by Kessler (2001a, b) on the Carrasco transect did show a mid-elevation peak (except for a monotonic decline in Melastomataceae), but individual maxima varied from elevations of 500 to 3000 m. Thus, while most taxa appear to show a humped richness-elevation relationship, the actual elevation of the peaks varies to such a degree that no single explanation seems plausible.

In conclusion, the hump-shaped relationship between elevation and species richness of neotropical birds appears to be caused by the overlap between two large regional species pools, i.e. lowland and highland. Although at a first glance the resulting pattern may appear to be driven by MDE, at least in our study this is not the case. As outlined by Grytnes (2003) close examination of the elevational distribution of empirical range midpoints in indispensable for correctly interpreting any correlation between observed richness and MDE predictions. We suspect that some of the elevational gradient studies that have supported MDE models simply on the basis of correlations of species numbers without considering range midpoints would have to be re-assessed. It also is important in this context to distinguish latitudinal from elevational patterns. Elevational gradients typically cover much shorter spatial distances, and local population-level processes, such as source-sink dynamics (Wiens and Rotenberry 1981, Pulliam 1988, Grytnes 2003), can therefore have a stronger effect on richness patterns. For example, it would be interesting to examine the reproductive output of bird populations along elevational gradients to establish if high species richness at the overlap between the lowland and highland faunas corresponds to an accumulation of sink populations. The high-elevation plateau documented by us further exemplifies that despite several decades of ecological research, elevational gradients are still not well understood and other unexpected patterns may remain to be discovered.

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