Detection of macro-ecological patterns in South American hummingbirds is affected by spatial scale

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Scale is widely recognized as a fundamental conceptual problem in biology, but the question of whether species-richness patterns vary with scale is often ignored in macro-ecological analyses, despite the increasing application of such data in international conservation programmes. We tested for scaling effects in species-richness gradients with spatially scaled data for 241 species of South American hummingbirds (Trochilidae). Analyses revealed that scale matters above and beyond the effect of quadrat area. Species richness was positively correlated with latitude and topographical relief at ten different spatial scales spanning two orders of magnitude (*ca.* 12 300 to *ca.* 1 225 000 km^2). Surprisingly, when the influence of topography was removed, the conditional variation in species richness explained by latitude fell precipitously to insignificance at coarser spatial scales. The perception of macro-ecological pattern thus depends directly upon the scale of analysis. Although our results suggest there is no single correct scale for macro-ecological analyses, the averaging effect of quadrat sampling at coarser geographical scales obscures the fine structure of species-richness gradients and localized richness peaks, decreasing the power of statistical tests to discriminate the causal agents of regional richness gradients. Ideally, the scale of analysis should be varied systematically to provide the optimal resolution of macro-ecological pattern.

Keywords: hummingbirds; latitude; scaling; species-richness gradients; topography; Trochilidae

1. INTRODUCTION

Patterns of species richness along latitudinal (Rohde 1992; Rosenzweig 1995), elevational (Lawton *et al.* 1987; McCoy 1990; Rahbek 1995, 1997) and longitudinal gradients (Cotgreave & Harvey 1994; Blackburn & Gaston 1996*a*) have become prime exemplars of large-scale pattern in macro-ecology (Brown 1995). The importance of scale in the resolution of biodiversity patterns has been widely recognized for decades (Hutchinson 1953; Whittaker 1977; Ricklefs 1987; Wiens *et al.* 1987; Wiens 1989; Orians & Wittenberger 1991; Cornell & Lawton 1992; Levin 1992; Schneider 1994; Andersen 1997; Taylor & Gaines 1999). In practice, however, most studies of species-richness gradients have tacitly assumed that patterns and generating mechanisms were similar at arbitrarily defined scales of analysis. Only recently have investigators tested this hypothesis at relatively small ecological scales (0.02 m^2 to 36 km^2) by systematically varying the cell size of the sampling grid (Palmer & White 1994; Böhning-Gaese 1997; Ault & Johnson 1998; Peltonen *et al.* 1998; Angermeier & Winston 1998; Carroll & Pearson 1998; Karlson & Cornell 1998; Ohmann & Spies 1998). Attempts to extend multiscale analyses to entire continents or oceans have been largely thwarted by the paucity of spatial data of sufficient quality and resolution, as well as by methodological and statistical obstacles. One notable exception was Lyons & Willig's (1999) analysis of species-richness gradients of South American bats and marsupials, based on nested quadrats of five sizes ranging in area from 1000–25 000 km^2. The largest of their quadrats, however, was more than an order of magnitude smaller than the equal-area grid of *ca.* 611 000 km^2, which has provided the spatial template for more than 50 papers on macro-ecology and conservation biology since 1994 (papers based on the data set of Blackburn & Gaston (1996*a,b*) and those listed in Williams (1999)). This immediately raises the question of whether macro-ecological patterns revealed using quadrats of this size or other arbitrary coarse-scale spatial formats change significantly with scale. More importantly, can the coarse-scale analyses now in vogue adequately characterize species-richness gradients and elucidate their underlying causes?

We addressed those questions by investigating the correlative relationships between the species richness of South American hummingbirds (*n* = 241 species) and geospatial variables (latitude and longitude) and topographical relief (hereafter topography) at ten spatial scales spanning two orders of magnitude (quadrat size varying from *ca.* 12 300 to *ca.* 1 225 000 km^2). These independent variables have been widely employed as surrogates for abiotic and biotic factors that influence species-richness gradients (e.g. Currie 1991; Rohde 1992; Cotgreave & Harvey 1994; Currie 1991; Kerr & Packer 1997). The strength of this approach lies in the straightforward nature of compiling the number of species in latitude–longitude quadrats (hereafter abbreviated as lat–long). We asked three hierarchical questions: (i) Is species richness correlated with latitude and longitude? (ii) To what extent does topography influence spatial patterns of species richness? (iii) Does the pattern of correlation between species richness and latitude, longitude and topography vary according to quadrat size? Finally, we address the implications of scaling for macro-ecological analyses and conservation programmes.

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2. METHODS

(a) *Choice of taxa*

Hummingbirds constitute one of the most speciose and arguably the most spectacular evolutionary radiation of birds. This nectarivorous–insectivorous clade (Bleiweiss *et al.* 1997) is eminently suitable for testing macro-ecological scaling hypotheses because the geographical ranges of species are relatively well known and the taxonomic inventory is believed to be nearly complete, as few new species have been discovered since 1950 (Graves 1993). Hummingbirds occur from Alaska (61° N) to Tierra del Fuego (55° S), but reach their greatest species richness in the equatorial Andes (figure 1). Seventy-six per cent of the 319 species recognized in Sibley & Monroe (1990) occur in South America.

(b) *Distributional data*

Distributional data were compiled from primary sources (i.e. museum specimens and documented sight records; museum sources listed in acknowledgements) for each of the 241 hummingbird species that occur in South America at a resolution of $1° \times 1°$ lat–long quadrats. Final maps for each species represent a conservative extrapolation of 'extent of occurrence' based on confirmed records and the spatial distribution of preferred habitat (for description of the methodology and sources see Fjeldså & Rahbek (1997, 1998)). We used the WORLDMAP computer program (v. 4.19.06, Williams 1998) to accommodate and overlay the hummingbird distributional data and to generate figure 1. Species richness was calculated for lat–long quadrats aligned at the equator and prime meridian at ten spatial scales ($1° \times 1°$, $2° \times 2°$, $3° \times 3°$, ... $10° \times 10°$). Quadrat centroids were used as spatial coordinates.

(c) *Topography*

We used topographical relief (maximum minus minimum elevation recorded in each quadrat) as a surrogate for topographical heterogeneity (Rahbek 1997). Elevational data, rounded to the nearest 100 m, were compiled from Operational Navigation Charts (1:1 000 000; published by the United States Defense Mapping Agency Aerospace Center, St Louis, MO, USA). These data are the most reliable estimates of elevational heterogeneity currently available in the public domain for the entire South American continent. Previous studies have considered elevational range as a surrogate for a broader measure of habitat heterogeneity (Currie 1991; Kerr & Packer 1997). Our use of topographical relief is conservative in that it tends to underestimate the true topographical heterogeneity at coarser spatial scales. We have avoided using extrapolation models of topographical relief because of the unacceptably high error associated with point estimation (Olsen & Bliss 1997).

(d) *Area*

Area *per se* has an indisputable influence on species richness that in principle must be dealt with in any analysis of species-richness gradients (Connor & McCoy 1979; Palmer & White 1994; Rosenzweig 1995; Rahbek 1995, 1997; Pastor *et al.* 1996; Lyons & Willig 1999). Within our region of analysis, the area of $1° \times 1°$ lat–long quadrats decreases from *ca.* 12 391 km^2 at the equator to *ca.* 7036 km^2 at 55° S. However, only 6% of the 241 species of hummingbird occur south of 35° S (quadrat area, *ca.* 10 273 km^2), meaning that the analytical results of our analyses were relatively similar whether or not quadrat area was taken into account. Nevertheless, because collinearity between quadrat area and latitude is significant, the effect of area on

species richness cannot easily be standardized at each scale of analysis without simultaneously obscuring the effect of latitude on species richness. Equal-area gridded maps circumvent this problem. The projection used to generate such maps, however, differs significantly from those used to produce traditional lat–long maps. This makes transfer of coordinate data obtained from specimen labels and published specimen records onto equal-area overlays more difficult than onto traditional lat–long maps. Moreover, the transfer of published range maps (lat–long) to equal-area grids is even more problematic, particularly from tiny distributional maps in field guides and other secondary literature sources (e.g. the approach used by Blackburn & Gaston (1996a,b) to compile their geographical database on New World birds). These problems are especially prevalent in the Andean arc region where dense aggregations of geographical range boundaries are commonplace. The use of equal-area maps also makes comparisons with previously published studies more difficult because of frame and scale shifts. For these reasons we believe the potential trade-offs, at the present time, argue for the continued use of lat–long quadrats for biodiversity studies.

The treatment of coastal quadrats is a far more serious problem in the analysis of species-richness gradients, whether or not lat–long or equal-area quadrats are used. One methodological option is to omit coastal quadrats from analyses (Rosenzweig 1995; Lyons & Willig 1999), but this procedure eliminates much of the important biological signal in South America, where biologically rich mountain ranges parallel the Caribbean coast of Venezuela and Colombia, the Atlantic coast of south-eastern Brazil, and the entire Pacific coastline. Information loss under such a data-censoring scheme is highly scale-dependent. For example, omission of coastal quadrats would result in sample size reductions of 15% for $1° \times 1°$ quadrats, 54% for $5° \times 5°$ quadrats, and 83% for $10° \times 10°$ quadrats.

In this study, we classified each $1° \times 1°$ lat–long quadrat as either continental (contained some land area) or oceanic (contained no land area, i.e. did not intersect the continental shoreline at a 1:1 000 000 map scale). The land area within larger-scale quadrats was estimated by summing the areas of the nested 'continental' $1° \times 1°$ quadrats. We then applied the Arrhenius power function (Arrhenius 1921), which posits that when sampling quadrats are positioned in a nested fashion, area (A) affects richness (S) in an exponential fashion, $S = cA^z$, and where the parameter c is the ratio of species richness to A^z, i.e. $c = S/A^z$ (Rosenzweig 1995). Given that z is similar between samples, one can standardize species richness to the same area by substituting the observed area and species richness into the following equation:

$$S_{\mathrm{sample1}}/A_{\mathrm{sample1}}^z = S_{\mathrm{sample2}}/A_{\mathrm{sample2}}^z, \tag{1}$$

$$S_{\mathrm{sample2}} = (S_{\mathrm{sample1}}/A_{\mathrm{sample1}}^z)/A_{\mathrm{sample2}}^z, \tag{2}$$

$$S_{\mathrm{sample2}} = S_{\mathrm{sample1}} \times (A_{\mathrm{sample1}}/A_2)^z. \tag{3}$$

In practice we used the equation

$$S_{\mathrm{adj}} = S_{\mathrm{obs}} \times (A_{\mathrm{max}}/A_{\mathrm{obs}})^z, \tag{4}$$

where S_{adj} was species richness adjusted by the maximum area (A_{max}) of quadrat size within a particular scale of analysis, S_{obs} was the observed species richness, and A_{obs} was the actual area of a given quadrat.

Pastor *et al.* (1996) and Rahbek (1997) calculated the actual species–area curve of each sample and then used the derived

Table 1. *Spatial and topographical determinants of hummingbird species richness*

scale	n	quadrant size (km²)[a]	latitude		longitude		topography		latitude × topography	
			F	r²	F	r²	F	r²	F	r²
1° grid	1689	12 308	1387.39	0.45***[b]	0.36	0.00	69.70	0.04***	159.88	0.09***
2° grid	457	49 225	277.09	0.38***	4.96	0.01	50.8	0.10***	29.71	0.06***
3° grid	216	110 729	114.12	0.35***	4.57	0.02	43.70	0.17***	12.50	0.06*
4° grid	129	196 784	69.44	0.35***	4.68	0.04	23.15	0.15***	8.35	0.06
5° grid	90	307 338	51.59	0.37***	2.35	0.03	15.79	0.15***	17.79	0.17**
6° grid	66	442 325	39.62	0.39***	3.69	0.06	17.77	0.22**	4.97	0.07
7° grid	49	601 674	26.48	0.36***	3.64	0.07	7.51	0.14	7.77	0.14
8° grid	40	785 268	22.81	0.38**	1.44	0.04	10.57	0.28*	3.35	0.08
9° grid	35	993 019	19.73	0.37**	0.39	0.01	12.46	0.27*	2.34	0.07
10° grid	29	1 224 797	17.33	0.39***	0.63	0.02	3.00	0.10	4.94	0.16
mean r²	—	—	—	0.38[c]	—	0.03	—	0.16	—	0.10
c.v. of r² (%)	—	—	—	7.6	—	75.4	—	47.1	—	45.3

[a] Maximum quadrat size by which species-richness values were standardized at each spatial scale (see § 2).
[b] Probability that the observed F-value is greater than or equal to the simulated F-value (9999 iterations in which species richness was randomly chosen from the pool of available values at each spatial scale). p-values were adjusted for error rate per variable: *$p < 0.05/10 = 0.005$; **$p < 0.01/10 = 0.001$; ***$p < 0.001/10 = 0.0001$.
[c] Independent variable has significant influence on species richness at all spatial scales.

Table 2. *Partial correlation analysis factoring out the influence of other independent variables in the model*

scale	n	quadrant size (km²)[a]	latitude		longitude		topography		latitude × topography		model with all variables	
			F	r²	F	r²	F	r²	F	r²	F	r²
1° grid	1689	12 308	472.50	0.22***[b]	0.02	0.00	527.22	0.24***	314.41	0.16***	616.46	0.60***
2° grid	457	49 225	49.49	0.10***	0.10	0.00	305.82	0.40***	185.31	0.29***	215.02	0.66***
3° grid	216	110 729	8.66	0.04*	0.34	0.00	202.40	0.49***	115.39	0.35***	123.12	0.70***
4° grid	129	196 784	3.07	0.02	0.12	0.00	151.86	0.55***	93.55	0.42***	89.28	0.74***
5° grid	90	307 338	8.87	0.09*	0.03	0.00	110.54	0.56***	69.05	0.44***	66.55	0.76***
6° grid	66	442 325	0.55	0.01	0.09	0.00	89.10	0.59***	61.59	0.49***	62.34	0.81***
7° grid	49	601 674	1.12	0.02	0.01	0.00	62.54	0.57***	49.76	0.51***	40.57	0.78***
8° grid	40	785 268	0.02	0.00	0.05	0.00	85.08	0.69***	46.80	0.55***	42.37	0.83***
9° grid	35	993 019	0.23	0.00	1.67	0.05	85.60	0.72***	46.07	0.58***	42.85	0.85***
10° grid	29	1 224 797	0.60	0.02	0.15	0.01	73.13	0.73***	51.81	0.66***	35.55	0.86***
mean r²	—	—	0.05	—	0.01	—	—	0.55[c]	—	0.44[c]	—	0.76[c]
c.v. of r² (%)	—	—	131.9	—	262.9	—	—	27.2	—	33.2	—	11.2

[a] Maximum quadrat size by which species-richness values were standardized at each spatial scale (see § 2).
[b] Probability that the observed F-value is greater than or equal to the simulated F-value (9999 iterations in which species richness was randomly chosen from the pool of available values at each spatial scale). p-values were adjusted for error rate per variable: *$p < 0.05/10 = 0.005$; **$p < 0.01/10 = 0.001$; ***$p < 0.001/10 = 0.0001$.
[c] Independent variable has significant influence on species richness at all spatial scales.

statistics to evaluate and remove the effects of area. This species–area approach, however, assumes that area is not correlated with any of the independent variables at any scale. Violation of the non-collinearity assumption can lead to error in hypothesis discrimination (Francis & Currie 1998). In this case, the high correlation between quadrat area and latitude, especially at our smallest scale of analysis ($1° × 1°$, $r² = 0.92$), prevents the application of a scale-specific approach. To ameliorate this problem, we pooled species-richness data over all ten scales of analysis (*ca.* 12 300 to *ca.* 1 225 000 km²), and tested for equal means in residuals (ANOVA), differences among sets of means in residuals (Tukey pairwise comparison test), trends in residuals (Pearson product-moment correlation), and homogeneity of variances in residuals (Scheffé–Box test). All tests

were non-significant ($p > 0.05$). We then used $z = 0.23$, derived from the pooled data and $\log S = z\log A + \log c$, to standardize species richness within each scale of analysis independent of latitude (correlation between area and latitude for the pooled data as low as $r² < 0.01$).

(e) *Statistical analyses*

We regressed species richness of quadrats on independent variables (latitude, longitude and topography) and on the latitude × topography interaction at each spatial scale (table 1). This procedure was repeated with partial regression analysis to factor out the influence of other independent variables (table 2). All independent variables were entered into a multiple regression model (species richness = constant + latitude + topography
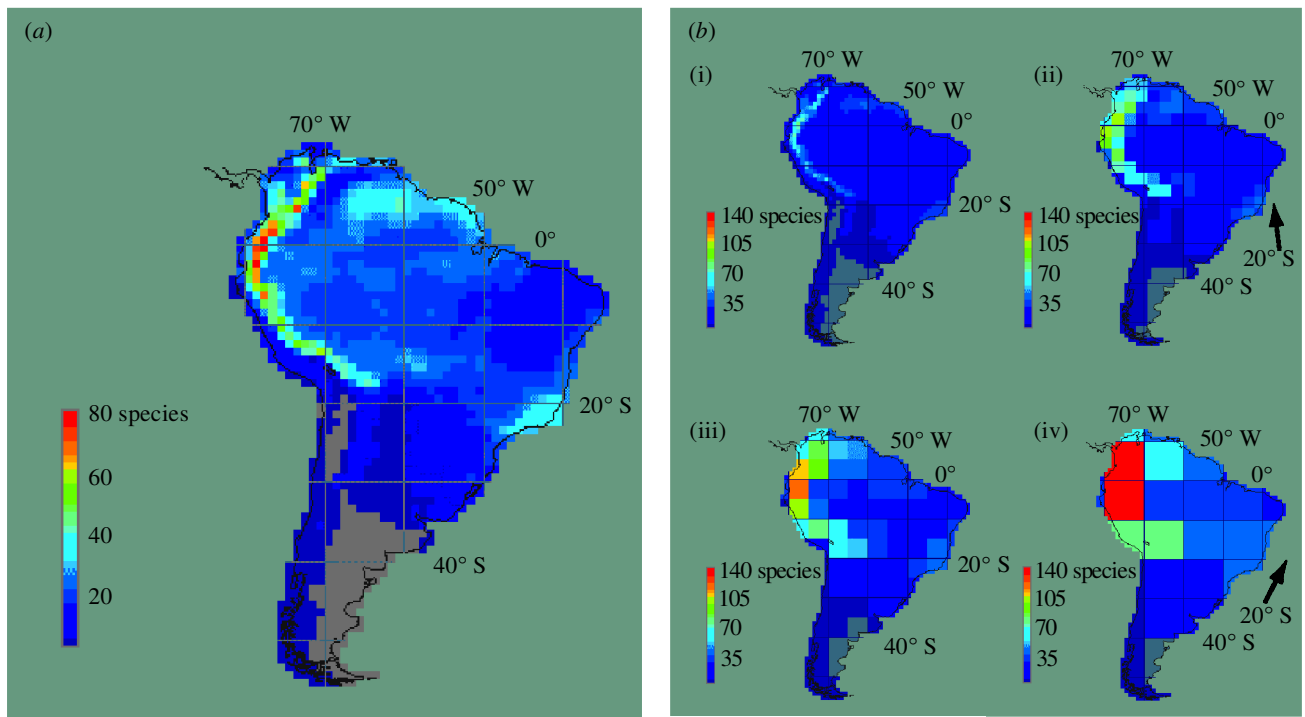
Figure 1. Spatial variation in species richness of South American hummingbirds (Trochilidae): (*a*) compiled at 1° × 1° scale; (*b*) compiled at (i) 1° × 1°, (ii) 3° × 3°, (iii) 5° × 5°, and (iv) 10° × 10° scales (different colour scales depicted in (*a*) and (*b*)). Note the excessive loss of information and the spurious extrapolation of high species densities in species-poor localities at coarser spatial scales. Grey areas illustrate quadrats supporting zero species.

+ latitude × topography) to estimate their power to predict species richness at different spatial scales.

Distributional assumptions of parametric regression tests are rarely met by macro-ecological data sets, and *p*-values reported in such studies are often unreliable. To avoid such problems, we report regression coefficients obtained by randomly permuting the dependent variable 9999 times (tables 1 and 2) (Legendre *et al.* 1998; see also Legendre *et al.* 1994). Spatial autocorrelation, an inherent quality of biogeographical data (e.g. geographical ranges of > 99% of South American hummingbird species overlap several to many adjoining 1° × 1° quadrats), increases the error in estimating the degrees of freedom and multiplies the risk of making type II errors. Although the relative importance of independent variables can be estimated by comparing the derived r^2-values, we emphasized non-significant *p*-values because the effects of spatial autocorrelation cannot be removed by simple permutation or randomization methods (Manly 1997).

3. RESULTS

Analyses revealed that the choice of quadrat size significantly influences the correlation between species richness and latitude, longitude, and topography (tables 1 and 2). Variation of r^2-values at different grid dimensions indicates that scale matters above and beyond the effect of quadrat area. Species richness was negatively correlated with latitude ($r^2 = 0.35$–0.45; coefficient of variation (c.v.) of $r^2 = 7.6\%$) at spatial scales spanning two orders of magnitude (table 1). Longitude was an insignificant predictor of species richness regardless of the scale of resolution ($r^2 < 0.07$; c.v. = 75.0%). The influence of topography on species richness fluctuated markedly with scale ($r^2 = 0.04$–0.28; c.v. = 47.1%).

Partial correlation analysis revealed a complex relationship between species richness, latitude, and topography (table 2 and figure 2). When the effects of topography were controlled, the predictive power of latitude decreased to insignificant levels ($r^2 < 0.05$) when quadrat area exceeded *ca.* 110 000 km² (table 2), perhaps due to collinearity between latitude and latitude × topography. Intriguingly, given the other variables in the model, both topography ($r^2 = 0.24$–0.73) and the latitude × topography interaction ($r^2 = 0.16$–0.66) explained a significant proportion of the conditional variation in species richness regardless of scale. A simple multiple regression model including latitude, topography and the latitude × topography interaction explained from 60 to 86% of the regional variability in species richness for quadrat areas ranging from *ca.* 12 300 to *ca.* 1 225 000 km² (table 2).

Although topography and latitude were generally uncorrelated ($r^2 < 0.03$; c.v. = 121.8%), hummingbird species richness appeared to be strongly associated with the interaction between topography and latitude (table 2). This influence was especially pronounced at low latitudes (11° N to 20° S) in the Andean region, where high elevations, rugged topography, and orographical precipitation patterns have resulted in perhaps the most complicated mosaic of distinctive terrestrial habitats on Earth, each supporting a characteristic hummingbird fauna. At the equator, hummingbird species are distributed from sea level to the snowline (0–5000 m). The elevational amplitude of the habitable zone decreases monotonically with latitude to Tierra del Fuego (55° S), where the single species of hummingbird is restricted to coastal habitats near sea level.
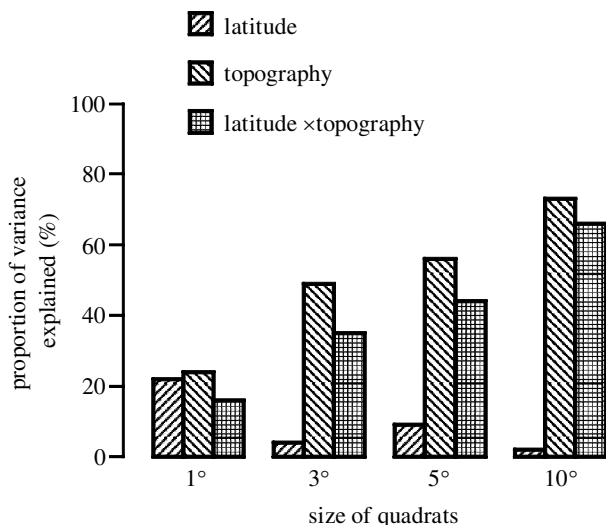
Figure 2. Conditional variation in hummingbird (Trochilidae) species richness explained by latitude, topography and the latitude × topography interaction. r^2-values are derived from partial correlation analyses (table 2).

4. DISCUSSION

The cause of latitudinal gradients in species richness is still hotly debated (Rosenzweig & Sandlin 1997; Rohde 1998). Hypotheses receiving the most attention follow three major themes: (i) energy-related variables correlated with latitude, e.g. available ambient energy, primary productivity, potential evapotranspiration, seasonality, solar radiation, temperature (Currie 1991; Rohde 1992; Wright *et al.* 1993; Francis & Currie 1998); (ii) area and the large-scale steady state between allopatric speciation and extinction within latitudinal bands exhibiting approximately homologous temperature (Rosenzweig 1995; see also Terborgh 1973); and (iii) geometric constraints on geographical range size and placement (Colwell & Hurtt 1994; Rahbek 1997; Willig & Lyons 1998; Lees *et al.* 1999; Colwell & Lees 2000). Bearing these proposals in mind, our findings are consistent with the hypothesis that the latitudinal species gradient is determined synergistically by a combination of variables correlated with both latitude and topography.

Differences in the relationship between hummingbird species richness and latitude at different quadrat sizes (tables 1 and 2) indicate that scale may not be easily accounted for by using species–area relationships as others have claimed (Palmer & White 1994; Pastor *et al.* 1996). Still, our results are robust and offer substantial support for the hypothesis that patterns of species richness as well as generating mechanisms are unlikely to be scale-invariant. The Andean region is the global centre of avian species richness, a pattern that becomes even more pronounced when the effects of area are accounted for (Rahbek 1997). More than half of all hummingbird species occur here and many endemic taxa are restricted to narrow elevational zones (Graves 1985, 1988). The influence of topography on species richness diminishes rapidly south of 20° S latitude as habitat diversity and timberline decrease. Though the influence of area on

species richness is one of macro-ecology's few unquestionable laws, biome area *per se* has a minor influence on hummingbird species richness. For example, the Amazonian tropical moist forest (*ca.* 5 million km^2) (Dinerstein *et al.* 1995) constitutes the largest biome in South America. Yet, $1° \times 1°$ quadrats in central Amazonia support only 16–25 species of hummingbirds, whereas species densities of quadrats straddling the eastern versant of the Andes, at equivalent latitudes, exceed 60 species (figure 1). In essence, hummingbirds exemplify the emergent biotic pattern in the Neotropics, in which speciation and β-diversity appear to be facilitated by topographical variation (Graves 1985), narrow homothermous elevational bands (Janzen 1967; Graves 1988; Rahbek 1997) and area (Rosenzweig 1995; Rahbek 1997).

(a) *Scale in macro-ecology and biodiversity conservation*

Because biodiversity data compiled at macro-ecological scales are increasingly used as the empirical basis of global conservation programmes (e.g. Dinerstein *et al.* 1995; Stattersfield *et al.* 1998), an assessment of the scaling bias in empirical and theoretical analyses is urgently needed. Many macro-ecological patterns are robust enough to be (re)discovered at coarse scales of resolution even when distributional data are transcribed from crude maps published in secondary literature sources. Although our results collectively suggest that there is no single correct macro-ecological scale for the investigation of species-richness gradients, finer geographical scales are generally preferred. Our data suggest that the species richness of most tropical birds and the relative importance of factors responsible for richness gradients cannot be adequately characterized at the coarser scales commonly used (e.g. Cotgreave & Harvey 1994; Eggleton *et al.* 1994; Blackburn & Gaston 1996*a,b*; Blackburn *et al.* 1998; Chown *et al.* 1998). For example, geographical ranges of South American hummingbirds are relatively small, averaging only 2.1 times the area of the *ca.* 611 000 km^2 quadrats employed in the aforementioned analyses. More than 68% of species have ranges smaller than a single such quadrat.

The averaging effect of quadrat sampling at coarse macro-ecological scales obscures the fine structure of species gradients and localized richness peaks (figure 1). Coarse-scale projections lead to predictions of extraordinarily high species richness in species-poor localities more than 500 km from true richness peaks. Such spurious extrapolations increase the risk of influential statistical outliers, and, most importantly, decrease the statistical power necessary to identify the causal agents of regional species-richness gradients (tables 1 and 2). Needless to say, coarse-scale maps of species richness are ineffectual for pinpointing areas of high endemism and inadequate for complementarity analyses for conservation purposes.

As a final note, we agree that time for cataloguing and mapping the Earth's biota is running out. Conservation programmes must rely, in large part, on macro-ecological analyses to identify and prioritize biologically important regions for protection (Dinerstein *et al.* 1995; Fjeldså & Rahbek 1997; Stattersfield *et al.* 1998). Nevertheless, the mode and quality of data collection (Gotelli & Graves 1996) and scale of analysis (e.g. Whittaker 1977; Wiens

1989; Cornell & Lawton 1992; Levin 1992; Angermeier & Winston 1998; Ohmann & Spies 1998; Lyons & Willig 1999) have a direct effect on the value and relevance of results. If macro-ecology is to provide the means to ameliorate and minimize the current biodiversity crisis, a thorough and scientifically based understanding of scaling effects must be obtained. We urge caution in generalizing from macro-ecological studies conducted at coarse spatial scales. Ideally, scale of analysis should be varied systematically to provide a better resolution of pattern and of the interrelationship among possible causal factors.

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