

INTER-SCALE RELATIONSHIP BETWEEN SPECIES RICHNESS AND ENVIRONMENTAL HETEROGENEITY: A STUDY CASE WITH ANTBIRDS IN THE BRAZILIAN ATLANTIC FOREST

Renata Durães^{1,2} & Bette A. Loiselle¹

¹University of Missouri-St. Louis and International Center for Tropical Ecology, 8001 Natural Bridge Rd, Saint Louis, MO, 63121, USA. ²E-mail: rrd32@umsl.edu

Resumo. – Relação entre riqueza de espécies e heterogeneidade ambiental entre diferentes escalas: um estudo de caso com formicariídeos na Mata Atlântica brasileira. – Heterogeneidade ambiental tem sido repetidamente apontada como um importante fator influenciando riqueza de espécies. Entretanto, o relacionamento entre estas duas variáveis tem sido tipicamente investigado entre escalas similares, e.g., como heterogeneidade de habitat em escalas locais ou regionais afetam diversidade alfa ou beta, respectivamente. Neste estudo, nós utilizamos Sistemas de Informação Geográfica (SIG) para investigar a relação entre a heterogeneidade ambiental em meso-escalas entre ≈ 80 –3000 km² e a riqueza local (escala de 1 km²) de formicariídeos (*Formicariidae latu sensu*) que ocorrem na Mata Atlântica brasileira. Cinco medidas de heterogeneidade ambiental foram examinadas (coeficiente de variação em precipitação, coeficiente de variação de elevação, variação de temperatura, número de tipos de solo e de vegetação). A distribuição espacial de riqueza apresentou padrões diferentes para espécies endêmicas e não-endêmicas, e, quando estes dois grupos foram analisados em conjunto, nenhuma correlação entre heterogeneidade ambiental e riqueza foi observada. Por outro lado, quando estes grupos foram analisados separadamente, correlações significativas foram observadas em todas as escalas examinadas. Correlações foram especialmente fortes para espécies endêmicas, e a proporção da variação em riqueza de espécies explicada por heterogeneidade ambiental aumentou com a escala utilizada.

Abstract. – Environment heterogeneity has been repeatedly identified as an important correlate of species richness. However, the relationship between these two variables has been typically investigated at comparable scales, e.g., on how local or regional habitat heterogeneity affects alpha or beta diversity, respectively. In this study, we used Geographic Information Systems (GIS) to investigate the relationship between habitat heterogeneity at the meso-scale-level (scales ranging between ≈ 80 –3000 km²) and local species richness (at the scale of 1 km²) of antbirds (*Formicariidae latu sensu*) occurring in the Brazilian Atlantic forest. Five measures of environmental heterogeneity were examined (coefficient of variation in precipitation, coefficient of variation in elevation, temperature range, number of soil types, and number of vegetation types). Endemic and non-endemic species presented distinct patterns of spatial distribution in richness and, when these two groups were analyzed together, no correlation between habitat heterogeneity and species richness was detected. On the other hand, when these two groups were analyzed separately, significant correlations were observed at all examined scales. Correlations were especially strong for endemic species, and the proportion of the variation in species richness explained by habitat heterogeneity increased with scale. *Accepted 17 December 2003.*

Keywords: Antbird, Atlantic forest, Brazil, biodiversity, GIS, Formicariidae, habitat heterogeneity, species richness.

INTRODUCTION

The search for proximate and ultimate causes of variation in biodiversity constitutes one of the most enduring debates in community ecology (e.g., Ricklefs 1987, Gaston 2000, Hubbell 2001). Among the many hypotheses advanced to explain patterns of biodiversity, some of the most important concern energy availability, evolutionary time, geometric constraints, and environmental heterogeneity in space and time (Gaston 2000, Kerr *et al.* 2001, Rahbek & Graves 2001).

Environmental heterogeneity has been long regarded as a primary factor promoting species diversity. Robert MacArthur and colleagues (MacArthur & MacArthur 1961, MacArthur & Wilson 1967) were some of the first to formalize this idea, offering an analytical explanation for why more complex environments should contain more species, and proposed that species-area relationships could be at least partly explained by the impoverishment in habitat diversity in small-sized islands. On the last decades, much work has been devoted to examine the role of habitat diversity *per se* in promoting species diversity. Many of these studies support the idea that increased habitat diversity leads to increased biodiversity (Ricklefs & Lovette 1999 and references therein), while others refute it (Marra & Remsen 1997, reviewed by Ricklefs & Lovette 1999).

This relationship has been investigated mainly at comparable scales, e.g., on how within-habitat diversity influences alpha diversity (e.g., Johnson 1975), or how habitat differences among regions influence beta diversity (e.g., Kerr *et al.* 2001, Rahbek & Graves 2001). On the other hand, less clear is how habitat diversity and species richness are related at different spatial scales; for example, how environmental heterogeneity at the meso-scale-level affects local species richness. Processes acting at different time scales can

be involved in this relationship. At a historical timeframe, environmental heterogeneity can affect speciation patterns, allowing population differentiation due to habitat specialization or following vicariant events (e.g., Qian & Ricklefs 2000). At an ecological timeframe, environmental heterogeneity may increase the number of available niches to be occupied, allowing species with different ecological requirements to overlap locally (Fraser 1998). Additionally, more diverse habitats may increase chances of colonists in finding suitable habitats and enhance population persistence by providing refuges for established individuals (Kohn & Walsh 1994, Ricklefs & Lovette 1999).

In this study, we address the question whether environmental heterogeneity at different meso-scales ($\gg 80\text{--}3000\text{ km}^2$) correlates with species richness at the local scale (in cells of $1\text{ km} \times 1\text{ km}$). Hence, rather than looking for specific environmental features that characterize regions with different richness patterns, we were interested in the role of environmental variation *per se* as a correlate of biodiversity. We used Geographic Information Systems (GIS) to answer this question, and antbirds (Formicariidae *latu sensu*) occurring in the Brazilian Atlantic forest as our study group. This group includes the families Formicariidae, Thamnophilidae, and Conopophagidae (Formicariidae are a paraphyletic clade and more likely represent two distinct families, Irestedt *et al.* 2002). Antbirds are well-suited for such study because they comprise an abundant and species-rich group in Neotropical forests. Moreover, they encompass a broad range of morphological and ecological characteristics (Sick 1997). For example, in terms of body size, this group includes some species such as the Star-throated Antwren (*Myrmotherula gularis*; $< 10\text{ g}$) to species such as the Variagated Antpitta (*Grallaria varia*; $> 120\text{ g}$). In terms of distribution range and habitat use, antbirds range

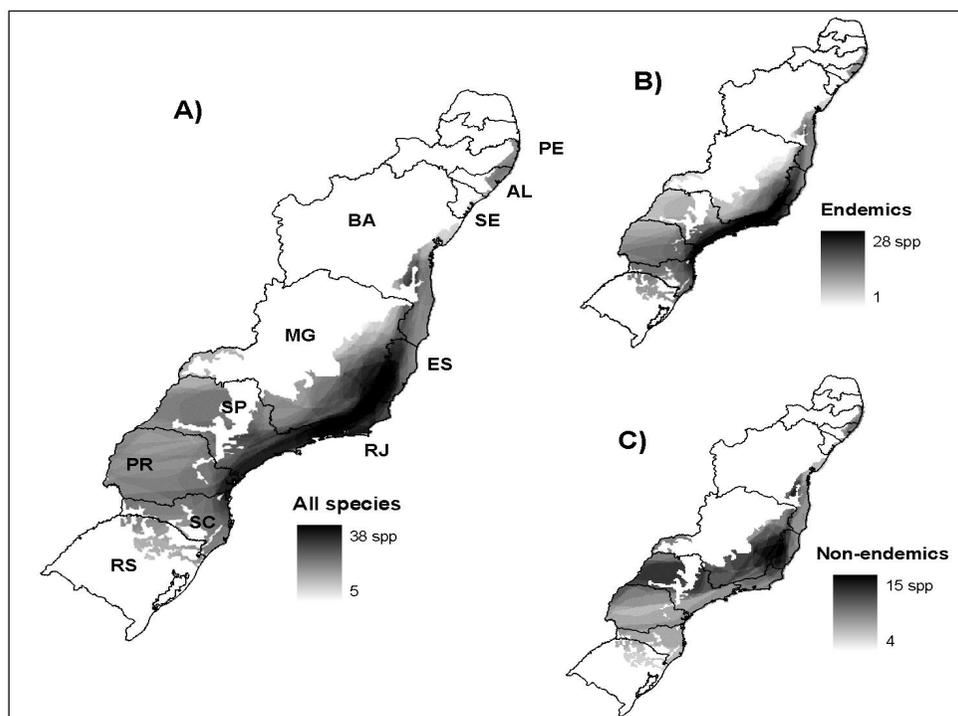


FIG. 1. Patterns of spatial distribution of antbird species richness in the Brazilian Atlantic forest: (A) all species (N = 59 species); (B) endemic species only (N = 37); (C) non-endemic species only (N = 22).

from species such as the Great Antshrike (*Taraba major*), an habitat-generalist with broad Neotropical distribution, to species such as the Restinga Antwren (*Formicivora littoralis*), with very narrow distribution range and habitat specificity. In Atlantic forest (AF), this group has diversified extensively and presents a large number of endemic species, several of these currently threatened by habitat destruction [e.g., Black-hooded Antwren (*Formicivora erythronotos*), Slender Antbird (*Rhopornis ardesiaca*), White-bearded Antshrike (*Biatus nigropectus*); Sick 1997, Collar *et al.* 1992].

The AF biome originally occupied 12% of the Brazilian territory (Oliveira-Filho & Fontes 2000), being the third largest biome in the country. It is considered as one of the 25 global biodiversity hotspots (Myers *et al.* 2000),

harboring 850+ bird species or ~ 47% of all Brazilian's avian richness (Machado & da Fonseca 2000), and encompassing at least five areas of bird endemism (Stattersfield *et al.* 1998). It is also one of the biomes most threatened by habitat destruction at a global level; it is estimated that as little as 5% of the original vegetation cover remains (SOS. Mata Atlântica 1998), and this remaining area presents itself highly fragmented or disturbed (Ranta *et al.* 1998, Oliveira-Filho & Fontes 2000, Silva & Tabarelli 2000). Thus, immediate management actions are required in order to preserve biodiversity in AF. Understanding the patterns of species distribution and the processes influencing these patterns can lend important insights about the most effective strategies in order to accomplish this task.

METHODS

In this study, we adopted a delimitation for the Brazilian AF based on vegetation maps obtained from World Conservation Monitoring Centre (WCMC, see below; Fig. 1). WCMC's vegetation map closely matches that of the Atlas Nacional do Brasil (IBGE 1992). This includes an area extending from north Rio Grande do Sul to north Pernambuco and covering $\approx 800,000 \text{ km}^2$, or $\approx 3000 \text{ km}$ in extension. Islands were not included in the analyzes.

Geographical analyses were conducted by using geographic information systems (GIS, ARC/INFO ver. 8.1 and 8.2, ESRI™, Redlands, California). Digital range maps for antbird species occurring in biome were obtained from Ridgely *et al.* (2003). This database is taxonomically up to date and presents species range information in the form of interpolated polygons. All species presenting a significant proportion of their range within the biome were included in this study. The bird range maps were transformed in digital coverage and overlaid to produce richness maps of endemic and non-endemic species, and for all antbird species combined. Richness maps were converted to grids of $\sim 1 \times 1 \text{ km}$ resolution (cell size of 0.01 units). The number of species per km^2 was defined as our measure of local species richness.

Environmental layers used to characterize habitat heterogeneity were: average annual precipitation (mm), annual mean temperature ($^{\circ}\text{C}$), soils, elevation (m a.s.l.), and pre-disturbance vegetation cover. Soils and vegetation layers were obtained as digital coverage from United Nations Environmental Program and WCMC. The soil map was produced by Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), in Brazil, and digitized at EROS Data Center, in Sioux Falls, South Dakota. The vegetation map was produced by Ministério da Agricultura at the Instituto

Brasileiro de Desenvolvimento Florestal (IBDF) and digitized by the Fundação Instituto Brasileiro de Geografia e Estatística (IBGE). Precipitation and temperature maps were obtained as digital coverages from the Worldclim database (<http://bnhm.berkeley.museum/gisdata/worldclim/worldclim.htm>). The elevation map was obtained as digital coverage from USGS EROS Data Center, Sioux Falls, SD (GTOPO30 model; <http://edcdaac.usgs.gov/gtopo30/gtopo30.html>). All these layers were edited to include only the area defined as the Brazilian AF and converted to grids in the same resolution ($\sim 1 \times 1 \text{ km}$) that the species richness grids.

One hundred points ($1 \text{ km} \times 1 \text{ km}$) with a minimum distance of 50 m between each other were randomly distributed within the delimitation map of AF, and local richness was determined for each of these points. Centered in each one of the points, we defined neighborhood areas as circles of three different sizes (radius of 5, 15, and 30 km). Habitat heterogeneity within these neighborhood areas was characterized in terms of coefficient of variation of average annual precipitation (precipitation CV), range of the annual mean temperature, number of soil types, number of vegetation types, and coefficient of variation in elevation (elevation CV). To correlate local richness to landscape-level habitat heterogeneity, we carried out forward stepwise multiple regressions with local richness as the dependent variable and the five estimates of habitat heterogeneity as the independent variables, at each scale. Stepwise regression was selected as the analysis method because the environmental variables were intercorrelated in several cases. The criterion for inclusion of an environmental variable in the model was set as $\alpha \leq 0.05$, and for exclusion as $\alpha \geq 0.10$. Data conformed to the parametric assumptions of normality and equality of variance among residuals. Statistical analyses were carried out in SPSS (2002).

RESULTS

A total of 59 species were included in the analyzes, among which 37 (63%) were considered as endemic and 22 (37%) as non-endemic to AF. Number of antbird species was 5–38 species/km² for all species, 1–28 for endemics, and 4–15 for non-endemics. Among the random points, average number of species present was 18.9 ± 5.8 , 10.4 ± 5.3 , and 8.5 ± 2.6 for all species, endemics, and non-endemics, respectively. Patterns of spatial distribution in richness differed for endemic and non-endemic species; the pattern of richness distribution for endemics resembled that of all species combined (Fig. 1 A–C). Endemic richness was concentrated along the coastline from Paraná to south Espírito Santo, matching the distribution of the mountain ranges of Southeast Brazil and their associated slopes. On the other hand, non-endemics species were concentrated in inner areas, notably in an area extending along west Espírito Santo, south Bahia, northwest Rio de Janeiro, and east/southeast Minas Gerais. Local richness of endemic and non-endemic species were negatively correlated, although not significantly ($r_s = -0.154$, $P = 0.127$).

AF presents pronounced variation in environmental features. Within the biome, elevation ranged from sea-level to >2800 m a.s.l. at the Pico da Bandeira; average annual precipitation varied between 400 to 2800 mm/year; annual mean temperature ranged from 8 to 25°C; 106 different soil types and ten different vegetation types (dense evergreen forest, evergreen mist forest, open evergreen forest, semi-deciduous seasonal forest, high-altitude relict vegetation, alluvial vegetation, coastal vegetation, pioneer vegetation in fluvial/alluvial areas, mangrove, and transitional vegetation) were identified. At the landscape level, these variables presented large variation as well. The coefficient of variation in elevation was 15.85 ± 27.94 , 26.44 ± 32.18 , and $9.89 \pm$

13.76 at neighborhood scales with 5, 15, and 30 m of radius, respectively. For the coefficient of variation in precipitation, these values were 1.50 ± 1.58 , 5.04 ± 11.37 , and 8.35 ± 19.88 . Temperature range values were 1.01 ± 0.91 , 2.42 ± 1.95 , and 3.57 ± 2.49 . Number of vegetation types were 1.26 ± 0.46 , 1.56 ± 0.69 , and 1.97 ± 0.90 . Number of soil types were 1.85 ± 0.64 , 2.86 ± 0.97 , and 4.49 ± 1.57 . Amount of variation significantly differed among neighborhood scales for all environmental variables ($F_{2,297}$ values: 10.673–137.179, all P -values < 0.001). Number of soil types, number of vegetation types, temperature range, and coefficient of variation in precipitation significantly increased with increasing neighborhood scale (Tukey HSD tests of post-hoc multiple comparisons: $P < 0.001$ in all cases). The coefficient of variation in elevation presented a different pattern; it was significantly larger at intermediate scales, but similar at neighborhood with 5 and 30 m of radius.

The stepwise linear regression including all species produced no correlation between environmental heterogeneity and local richness at any of the three neighborhood scales analyzed. On the other hand, when only endemic species were considered, correlations were highly significant and positive at all three neighborhood scales. The exact environmental variables retained in the final models varied among scales, but each one of the five variables was selected in at least one of the models; temperature range was the best environmental predictor of endemic richness at all three scales analyzed. The strength of the correlation between environmental heterogeneity and endemic richness increased from the smallest to the largest neighborhood scale, explaining between 28 to 43% of the variation in richness (Table 1).

When only non-endemic species were considered, significant correlations were observed as well at all three neighborhood

TABLE 1. Results of stepwise regressions analyzing the relationship between local richness of (A) endemic and (B) non-endemic antbird species in the Brazilian Atlantic forest and five measures of landscape-level environmental variation; in each case, N = 100 random points in all cases.

Neighborhood size	Variables retained	B	Adjusted r^2	P
Endemic species only				
r = 5 km	(1) Temperature range	1.89	0.277	< 0.001
	(2) Precipitation coefficient of variation	1.28		
	(3) Vegetation variety	2.22		
r = 15 km	(1) Temperature range	1.36	0.345	< 0.001
	(2) Elevation coefficient of variation	0.04		
r = 30 km	(1) Temperature range	1.11	0.425	< 0.001
	(2) Elevation coefficient of variation	0.09		
	(3) Soil variety	0.60		
Non-endemic species only				
r = 5 km	(1) Elevation coefficient of variation	-0.02	0.030	0.048
r = 15 km	(1) Temperature range	0.28	0.080	0.019
	(2) Elevation coefficient of variation	-0.02		
r = 30 km	(1) Temperature range	0.30	0.092	0.004
	(2) Elevation coefficient of variation	-0.06		

scales, and the degree of significance once again increased with neighborhood size. However, determination coefficients (r^2) were much weaker than those observed for endemic species. Moreover, negative rather than positive correlations were obtained with the coefficient of variation in elevation, at all three scales. Indeed, this coefficient was the only environmental variable retained in the final model at the smallest scale (radius = 5 km), although the determination coefficient was very low ($r^2 = 3\%$) and only marginally significant. Again, temperature range appears as an important correlate of species richness (Table 1).

DISCUSSION

Much effort has been devoted in identifying single factors as being globally responsible for spatial variability in species richness, but recent work has shown that factors structuring patterns of species richness are clearly scale-dependent. For example, the species-

energy hypothesis, according to which species richness is primarily determined by energy availability, has gained increasing support (e.g., Currie 1991). However, energy seems to be more limiting at broader (continental or inter-continental) scales, while within regions with similar energy inputs energy availability is a relatively poor predictor for species richness (Fraser 1998, Kerr *et al.* 2001). In contrast, habitat diversity has been repeatedly identified as an important correlate of species richness at local (Johnson 1975, Fox & Fox 2000) regional (Fraser 1998, Kerr *et al.* 2001), and even global scales (Guégan *et al.* 1998).

The positive relationship between habitat diversity and species richness has been attributed to a combination of increased number of ecological niches, speciation or specialization opportunities, and enhanced population persistence due to refuges (MacArthur & MacArthur 1961, Johnson 1975, Kohn & Walsh 1994, Fraser 1998, Ricklefs & Lovette 1999, Qian & Ricklefs 2000). In some cases, this

relationship is confounded with an effect of area: habitat diversity is likely to increase as area increases, and there is continuing controversy on the relative importance of each one of these variables in explaining species richness patterns (Burbidge *et al.* 1997). However, direct effects of habitat diversity on richness, independently of area, have been identified (e.g., Kohn & Walsh 1994); indeed, habitat diversity has often been demonstrated to predict richness better than area (Johnson 1975, Fox & Fox 2000). In this study, area was inherently controlled for by sampling grains with similar size. Moreover, because we examined the relationship between environmental heterogeneity and species richness at different spatial scales, a positive correlation due to area alone could not be intuitively expected *a priori*.

To our knowledge, this is the first study that examined the relationship between local patterns of species richness and habitat heterogeneity at the meso-scale level. Landscape-level habitat characteristics have been shown to influence species richness and abundance at the patch level (e.g., Graham & Blake 2001), and this study shows that this relationship can be extended to larger scales as well. Meso-scale habitat heterogeneity explained 28–43% of the variation in endemic species richness at a local scale, and 3–9% of the variation in non-endemic species richness. Interestingly enough, no correlation between habitat heterogeneity and species richness was observed when endemic and non-endemic species were analyzed together. Endemics and non-endemics presented contrasting patterns of spatial distribution of richness; indeed, numbers of species/km² in the two groups were negatively correlated, although not significantly. These results are insightful in demonstrating that, while habitat heterogeneity can be an important correlate of species richness, this pattern may disappear when groups with different patterns

of richness distribution are lumped in the analysis.

The negative correlations between the coefficient of variation in elevation and non-endemic species richness are probably artifacts due to the concentration of endemic species on the region with highest variation in elevation and the dissimilar spatial distributions of endemic and non-endemic species. In any case, these correlations were very low, and the slopes were very close to zero ($B = -0.02$ to -0.06 , Table 1).

Our results corroborate the idea that regional processes are important in structuring local patterns of species richness (Ricklefs 1987). The stronger correlation between habitat heterogeneity and endemism, as compared to richness of non-endemic species, also suggests that habitat heterogeneity had an important role in historical processes in Atlantic forest. Most of the richness in endemic species is concentrated along the mountain chains of Southeastern Brazil, whose uplifting certainly was involved in the speciation events occurred in the region. On the other hand, although correlations between habitat diversity and non-endemic species richness were also significant, the relationship was much weaker than for endemic species. This may suggest that the key mechanism by which habitat diversity influences species richness is by creating opportunities for speciation or specialization. Alternatively, this may indicate that, among Atlantic forest antbirds, endemic species are more habitat-specialized than non-endemic species and, because of this, more dependent on habitat diversity for local coexistence (e.g., Ricklefs & Lovette 1999); this hypothesis needs further examination.

Within the scale range investigated, the explanatory power of habitat heterogeneity increased with neighborhood size. Similarly, Fraser (1998) observed that the variation in vertebrate richness explained by environmen-

tal heterogeneity tended to increase with scale (10 to 120 km² grid-cell resolutions were analyzed). The author attributed this to the fact that the environmental datasets were too coarse to adequately represent biologically meaningful habitat heterogeneity at the smaller scales. Whether the increasing importance of habitat heterogeneity with scale detected in these two studies represents simply an artifact of insufficient map resolution or a true biological phenomenon remains to be explored.

Information is becoming increasingly available that allows large-scale tests of biodiversity hypotheses with high-resolution environmental and biological data (e.g., Kerr *et al.* 2001). Here, we suggest some directions for future studies. (1) Different groups can respond differently to habitat diversity; Ricklefs & Lovette (1999), for example, argue that habitat diversity might contribute less for species richness among specialists than among generalists. It would be thus interesting to contrast groups of species with different patterns of endemism and habitat requirements. (2) Because the strength of correlation between habitat heterogeneity and species richness tended to increase with scale, analyzes should be extended in order to examine how the observed relationship holds at different spatial scales. (3) Finally, this study was liberal in relation to the information about species ranges and some of the environmental layers used, and may depict historical rather than present-day scenarios. More detailed species data (e.g., point data for species occurrence) or up to date environmental data (e.g., present vegetation cover) could be used in order to examine how habitat destruction and fragmentation may have affected the results observed here. For example, a possible scenario is that the patterns of land-use in AF have led to a simplification or loss of suitable habitats used for many native species. In this case, we could predict that the loss of habitat

heterogeneity at large scales would have direct and negative consequences on biodiversity at local scales.

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