



SPATIAL VARIATION IN BAT SPECIES RICHNESS IN A FOREST-GRASSLAND TRANSITIONAL REGION OF SOUTHEASTERN SOUTH AMERICA

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Abstract: The latitudinal diversity gradient is the most well-known ecological pattern. Several hypotheses have been proposed to explain this biodiversity gradient. However, the predictors of species richness at continental scales may have different effects at regional scales, and even lose importance. Here we tested the effects of climate, energy, and habitat heterogeneity on the spatial variation of bat species richness in a forest-grassland transitional region, in southeastern South America. Our main goals were to assess which variables better explain bat species richness, and to analyze redundancy and complementarity among hypotheses. We generated three regression models, being each model related to a hypothesis, and compared R-squared among models. Then, we estimated redundancy and complementarity among hypotheses by partitioning the variation in species richness into unique and shared effects among hypotheses. Climate explained a larger proportion of the spatial variation of bat species ($R^2 = 0.97$, $p < 0.0001$), followed by heterogeneity ($R^2 = 0.94$, $p < 0.0001$), and energy ($R^2 = 0.93$, $p < 0.0001$), respectively. Variation partitioning analysis showed that climate explained the largest proportion of richness variation (83%). Energy and heterogeneity explained 55% and 51% of bat richness, respectively. The amount of variation explained uniquely by climate and heterogeneity were identical ($R^2 = 0.09$) whereas energy explained a small fraction of the variation ($R^2 < 0.01$). We conclude that climatic conditions coupled with habitat heterogeneity were the main predictors of bat richness in a forest-grassland transitional region and that the variables explaining regional richness gradient were the same at continental scale.

Keywords: climate hypothesis; energy hypothesis; heterogeneity hypothesis; mesoscale; spatial filters.

INTRODUCTION

Species richness along latitudinal gradients can be influenced by many factors, such as ecosystem productivity (Hawkins *et al.* 2003a), climate (Rahbek & Graves 2001), habitat heterogeneity (Kerr & Packer 1997), area (Rosenzweig 1995), time

for speciation (Mittelbach *et al.* 2007), tropical niche conservatism (Buckley *et al.* 2010), and high diversification rates in the tropics (Cardillo *et al.* 2005, Fine 2015). However, the magnitude and direction of the relationship between richness and environmental predictors can be different at regional scales (Keer & Packer 1997, Mittelbach *et*

al. 2001, Rahbek & Graves 2001). Therefore, the predictors of richness at continental scales may have different effects at regional scales (*e.g.*, Keer & Packer 1997), and even lose importance. Studies at regional scales are important because they control other predictors that vary widely over large latitudinal gradients. Furthermore, they allow assessing whether regional richness patterns have the same predictors as latitudinal patterns.

The most discussed ecological hypotheses as determinants of the species richness variation are energy and climate (*e.g.*, Currie 1991, Rahbek & Graves 2001, Hawkins *et al.* 2003a, 2003b, Currie *et al.* 2004). However, geometric constraints based on random species distributions over the geographic space could also generate the latitudinal pattern of species diversity without evoking any ecological process, the mid-domain effect (Colwell & Lees 2000). This hypothesis has been controversial in the ecological literature and, in several cases, the mid-domain effect produces different patterns than observed (Willig & Lyons 1998, Stevens *et al.* 2013). Furthermore, recently much more attention has been paid to the evolutionary effects of speciation and extinction as the causal drivers of the observed patterns of species diversity (Cardillo *et al.* 2005, Fine 2015, Harmon & Harrison 2015).

The energy hypothesis (also known as energy-richness hypothesis or the “more individuals” hypothesis) assumes that there is a positive relationship between species richness and the amount of energy entering the ecosystem (Currie *et al.* 2004). Thus, as more productive an area more individuals it can harbor and therefore more species, based on the assumption that high energy availability provides a broader resource base via trophic cascades. This relationship between productivity and richness is neither always linear nor positive. It could be negative or hump-shaped depending on the spatial scale (Mittelbach *et al.* 2001). Empirical support for the energy hypothesis has been found at regional and continental scales and for several groups such as mammals, birds, reptiles, amphibians, butterflies, beetles, and trees (Currie 1991, Hawkins *et al.* 2003a).

The climate hypothesis, also known as the “physiological tolerance hypothesis” (Currie *et al.* 2004) or “ambient energy hypothesis” (Hawkins *et al.* 2003a, 2003b), assumes that species richness is

a function of the species tolerance with climatic conditions. Under this hypothesis, species distributions are constrained by physiological requirements of organisms, and richness is higher in habitats with less environmental variation (*e.g.*, frost-intolerant plants and poor thermoregulators at low temperatures). Climate variables such as precipitation and temperature could also be interpreted as energy variables, since water and heat are fundamental factors to energy availability (*e.g.*, Hawkins *et al.* 2003a). Therefore, it is important to distinguish individual components of climate bearing in mind the mechanisms underlying the relationship between climate and species richness. Empirical support for this hypothesis has been found for several groups such as plants, insects, terrestrial vertebrates, and freshwater fishes (see Currie *et al.* 2004) at continental (Tello & Stevens 2010) and regional scales (Rabinovich & Rapoport 1975, Andrews & O’Brien 2000).

The habitat heterogeneity hypothesis assumes that as more heterogeneous an area is more species associated to different habitats are likely to be found there. Habitat heterogeneity (*e.g.*, number of ecoregions, topographic heterogeneity, forest height) has been acknowledged as a potential predictor of species richness but it has not been tested as much as energy and climate. Habitat heterogeneity is the main predictor of large-scale variation in mammal richness when energy availability is higher (Keer & Packer 1997). Empirical support for this hypothesis has been found for arthropods (Báldi 2008) and temperate mammals (Keer & Packer 1997) at regional scales, and small-ranged bats (Tello & Stevens 2010), and birds from Nearctic and Afrotropics (Hawkins *et al.* 2003b) at continental scales.

At continental scales, among these three hypotheses, energy has received the most empirical confirmation, explaining between 70 to 90% of the variation in species richness (Wright *et al.* 1993, Hawkins *et al.* 2003a). The climate variables, such as annual mean temperature and annual precipitation, are often positively correlated to species richness and influence directly the energy-related variables such as potential and actual evapotranspiration, PET and AET, respectively (Wright *et al.* 1993). However, at regional scales, temperature and precipitation can

also affect functioning of organism physiology through environmental stress (*i.e.*, colder and drier periods). If species are not able to tolerate low precipitation and low temperatures, for instance, these conditions may limit species distributions and therefore species richness (Rabinovich & Rapoport 1975).

The New World bats exhibit a marked latitudinal gradient of species richness (Willig & Selcer 1989, Willig *et al.* 2003, Stevens 2004), although the mechanistic basis of this pattern is still unclear. Some proposed hypotheses can be eliminated to explain latitudinal gradient in bat richness such as the area hypothesis (Willig & Bloch 2006) and the mid-domain effect (Willig & Lyons 1998). On the other hand, energy and climate explain most part of the richness variation (Patten 2004, Tello & Stevens 2010). Energy and seasonality explain different and complementary fractions of variation in bat richness in the New World whereas environmental heterogeneity explains a small fraction. Furthermore, richness of species with broad ranges is better explained by seasonality and energy whereas richness of species with small ranges is better explained by heterogeneity (Tello & Stevens 2010). That is a hint that regional analyses harboring different species compositions can identify different environmental effects on species richness that would be identified at continental analyses. Furthermore, importance of the predictors may also vary depending on the bat family under study (Patten 2004). Here, we examine how the bat species richness and its environmental components covary in space, and whether regional richness patterns have the same predictors as continental patterns. We expect covariation based on the three hypotheses described above. Thus, our goals are (i) to assess which hypothesis (energy, climate, or heterogeneity) better explains the variation in bat species richness at a forest-grassland transitional region in southeastern South America; (ii) to analyze which variables within each hypothesis are better related to bat richness; (iii) to compare predictor importance of each hypothesis across bat families (Molossidae, Phyllostomidae, and Vespertilionidae), and (iv) to analyze redundancy and complementarity among hypotheses.

MATERIAL AND METHODS

Data on species geographic range were obtained from the IUCN database (<http://www.iucnredlist.org/technical-documents/spatial-data>). All maps were clipped at the southeastern areas of South America delimited by the Paraná River at west and by the Grande River at north. This area encompasses an interface between forests (northward) and grasslands (southward), including Uruguay, southern Brazil (São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul States) and eastern Argentina (Misiones, Corrientes, and Entre Ríos Provinces). The main ecoregions (*sensu* Olson *et al.* 2001) within this area include Serra do Mar coastal forests, Cerrado, Alto Paraná Atlantic forests, Araucaria moist forest, Uruguayan savannas, and Espinal. The study area was divided in 466 grid cells of 0.5 by 0.5 degrees.

Environmental variables used as species richness predictors were obtained from online databases. The energy hypothesis included the effects of actual evapotranspiration (AET), solar radiation, and net primary productivity (NPP) on bat species richness. AET, a water-energy variable closely associated with plant productivity, is a measure of environmental productivity which is known to influence diversity gradients at a wide range of spatial scales (Hawkins *et al.* 2003a). NPP is a direct measure of productivity and it indicates how much carbon dioxide vegetation takes during photosynthesis minus how much carbon dioxide the plants release during respiration. Solar radiation is a measure of solar energy entering the ecosystem which is paramount to ecosystem productivity. AET and NPP were obtained from the Atlas of Biosphere (<http://www.sage.wisc.edu/atlas/>) at 0.5 degree spatial resolution. The climate hypothesis included the effects of annual mean temperature, temperature seasonality, and annual precipitation. These variables are expected to affect physiological conditions of organisms and they are related to richness variation in ecological gradients (Hawkins *et al.* 2003a, Tello & Stevens 2010). These variables and solar radiation were obtained from the Worldclim database version 2 (Fick & Hijmans 2017) at 10 min spatial resolution. The heterogeneity hypothesis included elevational

range, elevation, and forest height. Elevational range and elevation represent measures of habitat heterogeneity since high elevational range and high mean elevation are related to the existence of different conditions allowing species adapted to these conditions to coexist regionally (McCain 2007). Forest height is positively related to habitat complexity, *i.e.*, vertical variation in habitat physiognomy (August 1983). Mammal richness is positively related to habitat complexity by increasing potential food resources (August 1983). The elevational range was calculated from the difference between maximum and minimum altitudes within each grid cell. Maximum and minimum altitudes were obtained from the Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) available at https://topotools.cr.usgs.gov/GMTED_viewer/gmted2010_global_grid_s.php. Elevation was obtained from the Hydro-1K dataset (USGS 2001). Forest height was obtained from Simard *et al.* (2011). All variables related to the heterogeneity hypothesis were downloaded at 1 km spatial resolution. When necessary, variables were upscaled to 0.5 degree.

Environmental variables tend to be spatially autocorrelated which means that nearby cells do not represent independent spatial units increasing Type I error (Diniz-Filho *et al.* 2003). We checked the spatial structure of the residuals from the regression models using Moran's I coefficient calculated for 18 distance classes. When there was a spatial structure in the model residuals we used eigenvector-based spatial filters as additional predictors to avoid misleading interpretations (Diniz-Filho & Bini 2005). We selected the first 40 spatial filters and used them as predictors together with the nine environmental variables in a test model. We chose the first 40 filters based on a sensitivity analysis relating the accumulated number of filters and the R-squared values taking into account the Moran's I variation. After 40 accumulated filters, both the R-squared and the Moran's I stabilized (Figure 1). To not overcorrect the models, for each hypothesis we excluded those filters that were not statistically significant ($p > 0.01$) and did not affect the regression multiple correlation coefficients. After filter selection, we ran multiple regressions for each hypothesis to assess which one better explains the spatial variation of bat richness in a regional scale and

within each hypothesis which predictor is more relevant. We performed a variation partitioning analysis within each hypothesis to decompose the richness variation into two sets of predictors: (i) environmental predictors only and (ii) spatial filter (hereafter geographic space).

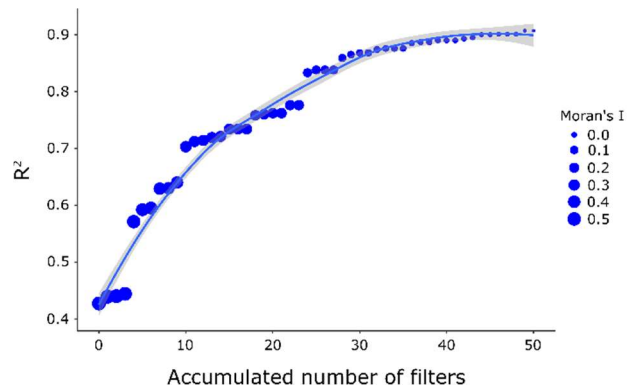


Figure 1. Relationship between the accumulated number of filters and the R-squared (R^2) values considering the Moran's I variation to assess the number of spatial filters where model explicability is maximum and spatial autocorrelation is minimal. Note that after 40 accumulated filters both R-squared and Moran's I stabilize. Figure generated using the package ggplot2 (Wickham 2009) in the R environment (R Core Team 2016). Gray area depicts the confidence interval.

To test which hypothesis better explains spatial variation of bat species richness, we generated three regression models, each model related to a hypothesis. Each model contained three variables without collinearity among them which was assessed by the variation inflation factor ($VIF < 10$ in all models). We compared R-squared of the models fitted for each hypothesis and the proportion of total explained by the environmental predictors only and by the geographic space only to assess which hypothesis better explains richness variation. However, these competing hypotheses are not mutually exclusive and they in fact act simultaneously on richness gradients (*e.g.*, Tello & Stevens 2010). Therefore, we explicitly estimate redundancy and complementarity among hypotheses by partitioning the variation in species richness into unique and shared effects among hypotheses. For this analysis we did not take into account the effects of spatial

autocorrelation because we are interested in the estimative of the proportion of variation explained by each hypothesis individually and not the estimative of the standard coefficients of the variable set. All spatial analyses were carried out with SAM 4.0 software (Rangel *et al.* 2010). This analysis was run considering all bat species and for the families Molossidae, Phyllostomidae, and Vespertilionidae.

RESULTS

Our species set was comprised by 65 bat species, harboring the families Furipteridae (N = 1), Thyropteridae (N = 1), Noctilionidae (N = 2), Emballonuridae (N = 4), Molossidae (N = 12), Vespertilionidae (N = 12), and Phyllostomidae (N = 33). Bat richness in the grid cells ranged from 1 to 65 species. The areas located northward (*e.g.*, Cerrado and Serra do Mar coastal forests) were richer than the areas located southward (*e.g.*, Uruguayan savannas and Espinal). This pattern was consistent across all bat families (Figure 2).

Climate explained a larger proportion of the variation of all bat richness ($R^2 = 0.97$, $F = 506.18$, $p < 0.0001$), followed by heterogeneity ($R^2 = 0.94$, $F = 219.23$, $p < 0.0001$) and energy ($R^2 = 0.93$, $F = 163.514$, $p < 0.0001$), respectively. When considering the proportion of explanation by the environmental predictors only (*i.e.*, excluding the effects of geographic space), climate was the better predictor of richness ($R^2 = 0.17$), whereas energy and heterogeneity explained a little proportion ($R^2 = 0.01$ and $R^2 = 0.03$, respectively). Among the predictors of climate, temperature seasonality was the most important variable, negatively related to species richness. Within the heterogeneity hypothesis, elevation was the most important variable related positively to richness. On the other hand, within the energy hypothesis, solar radiation was the most important predictor, negatively related to richness (Figure 3). Annual precipitation mean temperature, forest height, and AET were all positively related to bat richness. NPP and elevational range, however, were not related to richness (Table 1).

For Molossidae, all hypotheses seem to explain the same proportion (climate: $R^2 = 0.93$, $F = 193.14$,

$p < 0.0001$; energy: $R^2 = 0.92$, $F = 134.95$, $p < 0.001$; heterogeneity: $R^2 = 0.93$, $F = 172.31$, $p < 0.001$). However, when considering the proportion of explanation by the environmental predictors only, climate was the best predictor of molossid richness ($R^2 = 0.62$), whereas energy and heterogeneity explained a little proportion of the variation ($R^2 = 0.01$ and $R^2 = 0.03$, respectively). Within the climate hypothesis, temperature seasonality was the most important variable, negatively related to species richness (Table 1).

For Phyllostomidae, climate explained the largest proportion of richness variation ($R^2 = 0.97$, $F = 557.31$, $p < 0.0001$), followed by heterogeneity ($R^2 = 0.94$, $F = 205.67$, $p < 0.001$) and energy ($R^2 = 0.94$, $F = 180.13$, $p < 0.0001$), respectively. When considering the proportion of explanation by the environmental predictors only, climate was the best predictor of phyllostomid richness ($R^2 = 0.74$), whereas energy and heterogeneity explained a little proportion ($R^2 = 0.02$ and $R^2 = 0.03$, respectively). Among the predictors of the climate hypothesis, temperature seasonality was the most important variable and negatively related to phyllostomid richness (Table 1).

For Vespertilionidae, climate explained the largest proportion of richness variation ($R^2 = 0.90$, $F = 198.4$, $p < 0.0001$), followed by heterogeneity ($R^2 = 0.89$, $F = 170.65$, $p < 0.001$) and energy ($R^2 = 0.88$, $F = 156.47$, $p < 0.0001$), respectively. When considering the proportion of explanation by the environmental predictors only, climate was the better predictor of vespertilionid richness ($R^2 = 0.57$), whereas energy and heterogeneity explained a little proportion ($R^2 = 0.01$ and $R^2 = 0.03$, respectively). Among the predictors of the climate hypothesis, temperature seasonality was the most important variable being negatively related to vespertilionid richness (Table 1).

Variation partitioning analysis among the three hypotheses showed that climate explained most proportion of richness variation ($R^2 = 0.83$). Energy and heterogeneity explained 55% and 51%, respectively. Note that these values are different from the previous results because they did not include spatial filters as predictors. The amount of variation explained uniquely by climate and heterogeneity was identical ($R^2 = 0.09$) whereas energy explained a small fraction of the variation

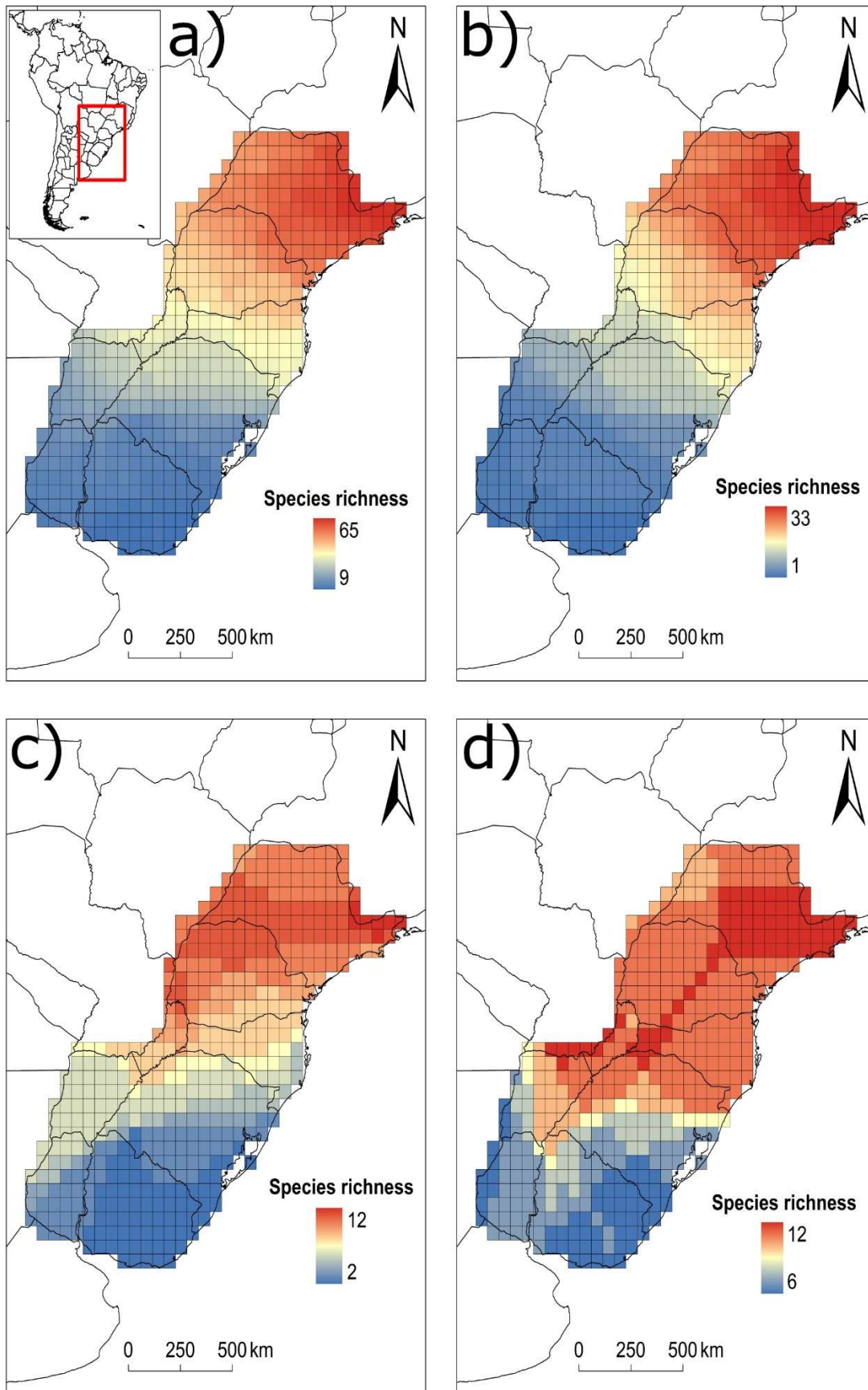


Figure 2. Maps showing the spatial variation on bat species richness across southeastern South America, a forest-grassland transitional region, derived from extent of occurrence polygons from IUCN dataset. a) all bat species, b) Phyllostomidae species, c) Molossidae species, d) Vespertilionidae species.

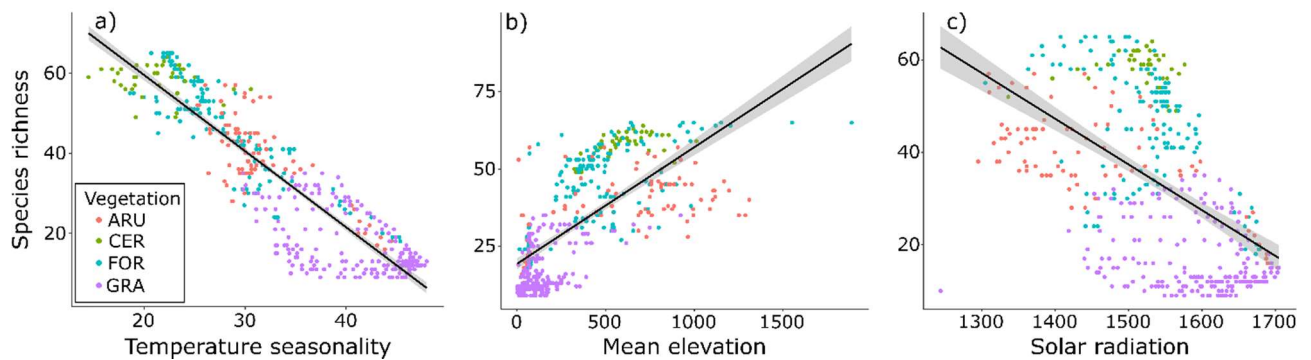


Figure 3. Linear regressions showing the relationships between bat species richness and (a) temperature seasonality ($R^2 = 0.81$, $p < 0.001$), (b) elevation ($R^2 = 0.48$, $p < 0.001$), and (c) solar radiation ($R^2 = 0.28$, $p < 0.001$). All models without spatial filters. Dot colors represent the main vegetation types in the southeastern South America. ARU = Araucaria Moist forests, CER = Cerrado, FOR = forested habitats (Serra do Mar coastal forests and Alto Paraná Atlantic forests), GRA = grasslands (Uruguayan savannas and Espinal).

($R^2 = 0.005$). All hypotheses exhibited some redundancy between themselves, except heterogeneity and energy, where the fraction explained by their interaction was smaller than 0.1% (Figure 4).

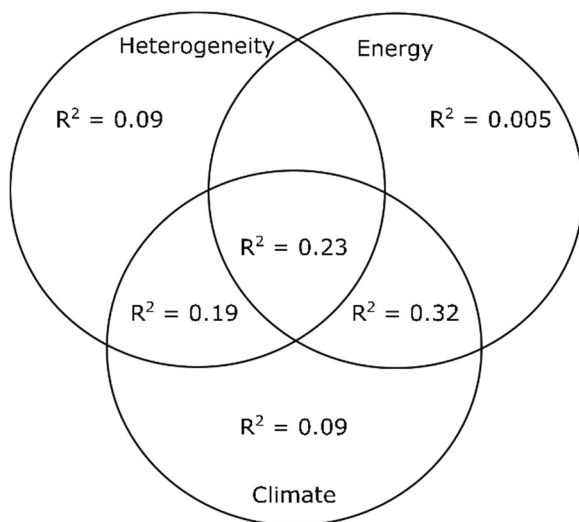


Figure 4. Venn diagram showing the variation partitioning among three hypotheses (heterogeneity, energy, and climate) to explain the variation in bat species richness gradient in the southeastern South America. R-squared values represent unique (*i.e.*, complementarity) and shared (*i.e.*, redundancy) explanation for bat richness variation. $R^2 < 0.001$ not shown.

DISCUSSION

Bat species richness in the forest-grassland gradient is affected mainly by variables related to climate, especially temperature seasonality. That is, physiological tolerance of species to extreme

climatic conditions (Rabinovich & Rapoport 1975) seems to be the main mechanism generating spatial variation in bat richness at a regional scale. However, when estimating complementarity and redundancy among hypotheses, the unique effects of climate and heterogeneity explained the same proportion of bat richness. Although the proportion of explanation was similar across hypotheses, energy was almost fully redundant with climate, exhibiting the highest R-squared of all fractions of the variation partitioning analysis. Therefore, the signal of energy on bat richness gradient should reflect the combined effects of temperature and rainfall.

Hawkins *et al.* (2003a) showed that water variables, such as annual precipitation, tend to be best predictors of plant richness gradient when the analysis is restricted to tropical and subtropical areas whereas water-energy variables, such as AET, dominate in temperate areas. Here, bat richness gradient in a geographic scope within tropical and subtropical areas was also predicted by water variables (Table 1) but the strength of temperature seasonality was higher in all cases analyzed. The molossid richness gradient was related exclusively to temperature variables and not to annual precipitation, indicating that thermoregulatory effects should be the main mechanism explaining the observed richness gradient for this family. Similar pattern was found for passerine birds in Argentina where temperature was the best predictor of bird richness (Rabinovich & Rapoport 1975). Mammal richness gradient in southern Africa (15° to 35° S), a latitudinal extent similar to the extent considered here (19° to 35° S), was also

better predicted by temperature (annual temperature and thermal seasonality) than by energy variables (Andrews & O'Brien 2000). It seems that, at regional scales in tropical-subtropical gradients, vertebrate richness is better predicted by temperature than energy variables. The major relationships between temperature and richness found here seem to be opposed to the main global relationships between water, energy, and richness found for several vertebrate groups (see Hawkins *et al.* 2003a). However, seasonality was an important predictor of bat species richness both at a continental scale (Tello & Stevens 2010) and at a regional scale (Andrews & O'Brien 2000, Stevens 2013). Therefore, coupled with the results found here, seasonality seems to be the major predictor of bat richness gradient regardless the scale considered but not for other vertebrate groups. The climate hypothesis assumes that reproduction and growth rates are greater at higher temperatures and less at seasonal environments, leading to larger populations in lower latitudes. Less seasonal environments allow bats to deviate metabolic energy that would be used for thermoregulation to growth and reproduction (McNab 1982).

Turner *et al.* (1987) found that hours of sunshine was a good predictor of British butterfly richness. Here, opposed to our expectations, solar radiation was negatively related to species richness. Solar radiation is the main input of energy into the ecosystems and it is expected to affect productivity (Monteith 1972). Opposed to the richness trend, solar radiation was higher in the south than in the north of the studied region. Solar radiation was a better predictor of richness than AET, except for Molossidae. However, solar radiation *per se* does not affect species richness. The energy input provided by solar radiation must be coupled with water availability. In areas where solar radiation was high, precipitation levels were low. Furthermore, this negative relationship may be an artifact of the spatial scale considered here. Over a continental scale it is likely that solar radiation is positively related to richness but this assumption is yet to be tested. As far as we know, this is the first study to relate solar radiation to species richness gradients in a regional scale.

Similar to climate, habitat heterogeneity also explains a unique variation of bat richness

gradient. Effects of habitat heterogeneity were better predicted by elevation and forest height, respectively. This pattern was consistent across all bat families. Elevational range was not a good predictor of richness gradient. However, it was a good predictor of bat richness in North America (Patten 2004), but the effects of elevation and elevational range on bat richness are presumed to be similar. Habitat heterogeneity also predicts the regional bird diversity in northern South America (Rahbek & Graves 2001) and Argentina (Rabinovich & Rapoport 1975) and the global richness of riverine fishes (Guégan *et al.* 1998). In some cases, habitat heterogeneity affects species richness in areas of high productivity (Kerr & Packer 1997). In our case, productivity was not as important as climate and habitat heterogeneity in predicting bat richness. Therefore, elevation and forest height provide different microhabitats which allow species to adapt to different environmental conditions and habitat use. Indeed, measures of habitat heterogeneity, such as forest height, can also explain why there is less bat species in the southern grasslands than in the northern forests. These mechanisms allow species to coexist regionally.

Regional analyses on richness gradient are important to distinguish the predictor effects that may be confounded over continental scales (Kerr & Packer 1997). Here we showed that bat species richness in a forest-grassland transitional region is associated with temperature seasonality, mean temperature, annual precipitation, elevation, forest height, AET, and solar radiation, which is consistent with previous analyses elsewhere (Hawkins *et al.* 2003a, Patten 2004, Tello & Stevens 2010). We conclude that climatic conditions, coupled with habitat heterogeneity, were the main predictors of bat richness in this forest-grassland transitional region. These effects are related to the original hypothesis proposed by von Humboldt (1808) to explain the latitudinal richness gradient (the "freezing tolerance" hypothesis) and they can be identified at both regional and continental scales.

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Table 1. Multiple regressions coefficients corrected through spatial filtering for each hypothesis (heterogeneity, energy, and climate) used to explain the spatial variation of bat species richness in a forest-grassland transitional region, in southeastern South America. Analyses were run considering the whole bat species and by each family (Molossidae, Phyllostomidae, and Vespertilionidae). Bold values indicate statistical significance ($p < 0.05$).

Hypotheses	Whole			Molossidae			Phyllostomidae			Vespertilionidae		
	p-value	VIF	Std. Coeff.	p-value	VIF	Std. Coeff.	p-value	VIF	Std. Coeff.	p-value	VIF	Std. Coeff.
Heterogeneity												
Elevation	<0.001	3.4	0.26	<0.001	3.64	0.24	<0.001	3.29	0.21	<0.001	2.99	0.18
Elevational range	0.49	1.4	-0.01	0.34	1.44	0.01	0.09	1.44	-0.025	0.74	1.41	-0.006
Forest height	<0.001	2.8	0.1	<0.001	2.81	0.08	<0.001	2.76	0.1	<0.001	2.56	0.12
Energy												
AET	<0.001	2.6	0.14	<0.001	2.62	0.17	<0.001	2.7	0.15	<0.001	2.21	0.1
NPP	0.81	1.4	-0.004	0.99	1.43	<.001	0.94	1.41	-0.001	0.47	1.3	0.01
Solar radiation	<0.001	4.8	-0.2	0.12	5.59	0.05	0	5.22	-0.25	<0.001	2.35	-0.17
Climate												
Mean temperature	0.01	2.2	0.03	0.001	3.88	0.08	0.02	3.39	0.04	0.81	2.24	0.005
Temperature seasonality	0	4.7	-0.67	0	2.3	-0.94	0	2.21	-0.96	0	1.82	-0.8
Annual precipitation	0	3.7	0.14	0.9	4.02	0.003	<0.001	3.7	0.09	<0.001	1.51	0.17

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