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REPORT

Null models and spatial patterns of species richness in South American birds of prey

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Abstract

In this paper, we used geostatistical approaches to describe bi-dimensional spatial patterns in species richness of South American birds of prey (Falconiformes and Strigiformes). They indicated strong spatial patterns both across latitude and longitude, for the two groups. These patterns were then correlated with those expected by a bi-dimensional null model constructed to take into account South America continental edges. As considerable departures from the null model were observed, there may be other ecological or evolutionary explanations for spatial patterns in species richness. Variation seems to be related to habitat heterogeneity across the continent, especially when considering differences between habitats in the central and south-eastern portion of the continent and in the Andean region. This supports previous conclusions that habitat type and heterogeneity affect species richness and abundance at different spatial scales.

Keywords

Null models, species richness, South America, Falconiformes, Strigiformes, geostatistics, variograms.

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INTRODUCTION

Latitudinal gradients in species richness are one of the most discussed features in ecology and biogeography. Various mechanisms have been proposed to explain them, including correlated responses of richness to gradients in competition, mutualism, predation, spatial patchiness, environmental stability and predictability, productivity and energy, available area for colonization, and ecological and evolutionary time (Rohde 1992, 1997; Kaufman 1995; Rosenzweig 1995; Rosenzweig & Sandlin 1997; Willig & Lyons 1998; Taylor & Gaines 1999). In spite of this, a consensus about the primary causes for latitudinal gradients in species richness is yet to be reached (Colwell & Lees 2000a; Rahbek & Graves 2000).

Recently, the study of spatial variation in species richness turned in a new direction, prompted by the recognition that peaks in species richness may be associated with the geometry of species' ranges in relation to continental boundaries, the so-called 'mid-domain effect' (Colwell & Lees 2000a). These ideas have been particularly stimulated by the application of analytical methods and computer-intensive simulation strategies to generate null models for variation in species richness at large geographical scales (Colwell & Hurt 1994; Lyons & Willig 1997, 1999; Willig & Lyons 1998; Lees *et al.* 1999; Colwell & Lees 2000a; Colwell & Lees 2000b; Jetz & Rahbek 2001). In a simple one-dimensional model (i.e. involving only latitude), these null models usually predict a convex, symmetrical pattern, with a peak at the middle of the latitudinal extent of the continent.

Willig & Lyons (1998) proposed a simple analytical null model for latitudinal gradients, in which the species richness at a point P, defined by a pure stochastic process, is a function of its distance to northern and southern endpoints of the continent, defined by the proportions p and q. The species richness in P is then given by $2pqS$, where S is the total species richness in the continent (the species pool). Willig & Lyons (1998) fitted this model to variation is species richness for new world bats and marsupials, finding strong agreement between the data and the model, with r^2 usually larger than 60%.

More recently, Bokma *et al.* (2001) extended the previous model to a bi-dimensional space, by including relative distances from P to western and eastern continental boundaries (s and t). So, the species richness expected at P by chance alone is then given by $4pqstS$. Bokma *et al.* (2001) also constructed a null model based on speciation, migration and extinction that produced results very similar to Willig & Lyons's (1998) model, specially if South and North America were analysed independently, because of the area constriction created by Central America in the middle of the continent. They tested both models using data from New World mammals, and again they found a high correlation between observed and predicted species richness in South America (but not for Central America and North America). Although other null models based on randomization of geographical ranges or latitudinal extents across continent are available today and permit a clearer evaluation of their assumptions (Colwell & Hurt 1994; Bokma *et al.* 2001; Jetz & Rahbek 2001), the main advantage of the bi-dimensional extension of Willig & Lyons's (1998) analytical null model is its computational simplicity.

The purpose of this paper is to apply this recently developed bi-dimensional null model to account for species richness variation of birds of prey (Falconiformes and Strigiformes) in South America. More specifically, we used geostatitical techniques (semi-variograms and kriging maps) to analyse spatial patterns of overall species richness in these two groups and correlate these patterns with those expected by the bi-dimensional null model constructed to take into account South America continental edges. If patterns in species richness are close to those obtained under a null model, this may indicate that distribution of species is random or that factors controlling their distribution are random. On the other hand, departures from randomness demand ecological or evolutionary explanations. We then introduce habitat type as an additional effect into the analyses because many authors have shown how habitat type and heterogeneity affects species richness and abundance, at different spatial scales.

MATERIALS AND METHODS

Data

The geographical distribution of species was obtained from Dunning (1987), Sibley & Monroe (1990) and Del Hoyo *et al.* (1994). The geographical ranges (extent of occurrence—*sensu* Gaston 1994) of 80 species of Falconiformes and 33 species of Strigiformes were re-drawn on a standardized map of South America (Azimuthal projection, scale 1 : 40 000 000) covered by a grid with 780 quadrats of *c.* 135 × 135 km. The presence (1) or absence (0) of each species in each cell of the grid map was recorded, and species richness for each quadrat was estimated by counting the number of species present in each cell. For the Falconiformes and Strigiformes, respectively, 82% and 77% of the species analysed here possess more than 90% of their range within South America only, and we considered this when fitting null model (see below). The spatial coordinates of each quadrat were then associated to each value of species richness. Predominant biome type was also assigned to each quadrat in the grid, based on a UNESCO vegetation map that divides South America into 30 habitat types (biomes) (UNESCO 1981).

Spatial patterns in species richness

A semi-variogram represents the relationship between average dissimilarity between quadrats as a function of their separation distance (Rossi *et al.* 1992; Maurer 1994) The semi-variance (γ) is given as

$$\gamma = \frac{1}{2} N(h)\Sigma[Z(x+h) - Z]^2,$$

where γ is the estimated semi-variance for the lag h, $N(h)$ is the number of pairs of points separated by a given spatial distance class (the lag h) and Z is the variable analysed (in this case, species richness) at a point x in geographical space.

The most important parameters in the semi-variogram are: (1) the range of autocorrelation, which gives the distance within which the samples remain autocorrelated; (2) the sill, which indicates the maximum semivariance achieved in the semivariogram; and (3) the nugget effect, the intercept of the estimated function, which represents the unresolved small-scale spatial variation or the sampling error. These parameters were fitted to observed semi-variograms and used to generate an interpolated surface of richness variation by kriging (Rossi *et al.* 1992; Maurer 1994). The geostatistical procedures were performed using GeoEAS software, from U.S. Environmental Protection Agency.

Generation of expected richness: the application of the null model

Due to strong autocorrelation between adjacent quadrats and computational difficulties associated with parameter estimation of the null model for all the 780 quadrats covering the South America map, we used a sample of 32 quadrats in the grid, situated approximately 675 km apart, to generate expected richness values under this null model (Fig. 1a). This procedure tends to minimize bias in Type I error of correlation analyses between spatially structured variables depending on the magnitude of spatial pattern in species richness (Bini *et al.* 2000).

In this paper, we chose the analytical null model of Willig & Lyons (1998), extended to a bi-dimensional space, after consideration of its computational simplicity and the difficulties associated with creating biologically realistic bi-dimensional geographical ranges for a given species group using randomization procedures (Bokma & Mönkkönen 2000; Colwell & Lees 2000b; Koleff & Gaston 2001). Of course, Willig & Lyons' (1998) model also has assumptions, i.e. that there is a uniform distribution of geographical range

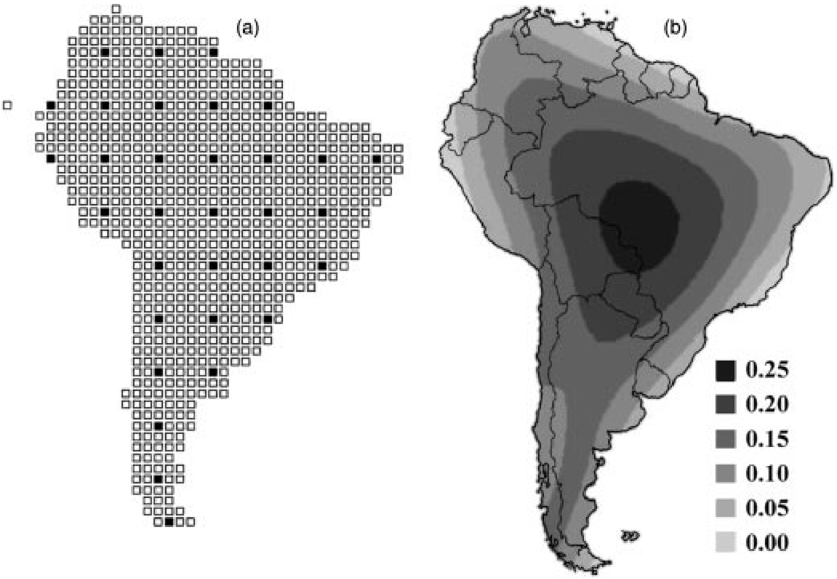

Figure 1 Quadrats used to define the bi-dimensional extension of Willig & Lyons's (1998) null model (a) and proportion of continental species pool (4pqst) interpolated along South America (b) (see text for details).

midpoints and that the maximum possible range of the species may be equal to the full area of the domain.

The values of *pqs* and *t* in this null model were calculated for each of the 32 quadrats as their relative position within South America in north, south, east and west directions, respectively. It is important to note that each of these values was estimated from each central quadrat to the immediate continental boundary, in such a way that continent shape has a direct effect on the expected richness, as in the evolutionary model of Bokma *et al.* (2001). More importantly, in this case, *a priori* definition of the domain (i.e. South America) does not change the expected proportion of the continental pool. So, although we are analysing only South America and exclude Central and North America, expectation of richness is not altered by this decision (although the definition of the species pool can be—see Discussion).

Under this null model, the richness peak (proportion of species pool) is found in the middle of the continent (Fig. 1b). For the Falconiformes, the continental species pool *S* used to calibrate the model was 80 species and for Strigiformes the *S*-value was 33 (Sibley & Monroe 1990; Del Hoyo *et al.* 1994). The squared correlation coefficient (r^2) between expected and observed species richness in the 32 quadrats permits an evaluation of the agreement between the data and the model.

However, it is important to note that, by its original definition (Colwell & Hurt 2000a; Jetz & Rahbek 2001), the mid-domain effect must appear for taxa endemic to the analysed region, whose hard boundaries constrain geographical range and create the peak of species richness at the middle of the area. Although most of the geographical ranges of the species analysed here are within South America only (and all midpoints are within the latitudinal South American domain), there will nonetheless be bias caused by these few exceptions. So, we repeated the analyses excluding species whose geographical ranges extend beyond South America, rescaling the species pool appropriately.

The effect of habitat type on spatial patterns in species richness

The effect of biome type was measured using a categorical expression of biomes along the continent, analysed as a factor in a model II single classification analysis of variance (anova) (Sokal & Rohlf 1995). The response variable was the species richness in each quadrat, for the two groups. The intraclass correlation coefficient estimates the relative magnitude of average richness variation within and between these biomes. Because biomes were also patterned in the space, up to a third-order polynomial expansion of geographical coordinates (latitude and longitude) of quadrats was also used as covariates in the model, in a combined anova/trend surface analysis (Legendre & Legendre 1998).

RESULTS

The semi-variograms for the Falconiformes and Strigiformes revealed strong spatial patterns for species richness in the two groups, and were well fitted by linear (for Falconiformes) spherical (Strigiformes) models (Fig. 2). The nugget effects were small in the two analyses (less than 10% of the maximum semi-variance–sill), indicating that there is small portion of unresolved spatial variability in richness at small scales. The range of the semi-variograms, however, indicated clear spatial structures at very large spatial scales. For Falconiformes, there is no clear

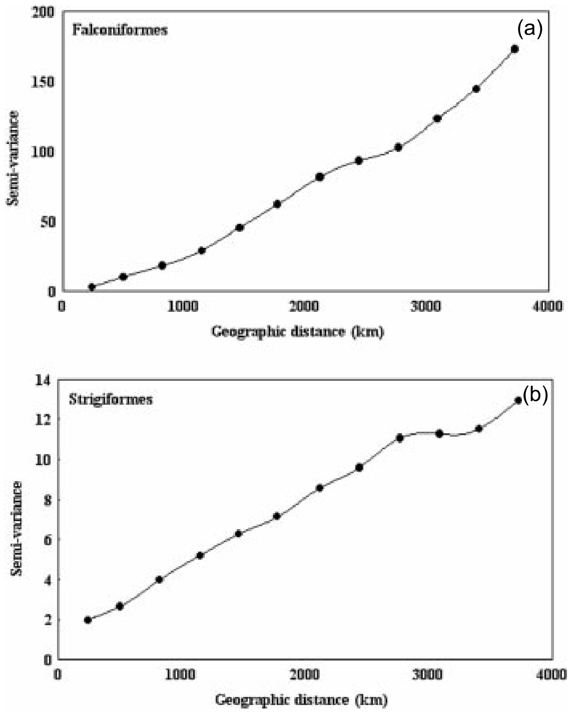

Figure 2 Semi-variograms for species richness along 780 quadrats covering South America. (a) Falconiformes and (b) Strigiformes.

stabilization of semi-variance (Fig. 2a), and a maximum of 4000 km was used as the sill parameter for fitting a bi-dimensional surface by kriging. For the Strigiformes, the fit was made by a spherical model, the range was set to 3000 km, a distance at which a slight stabilization of the semi-variance was observed. A cross-validation procedure indicated that 97.8% and 92.5% of the variance of the fitted surface was explained by the chosen model and parameters for Falconiformes and Strigiformes, respectively. So, difficulties in fitting a model to the observed semi-variogram should not have a major impact in the surface estimation (see below).

Patterns of species richness for the two groups are similar ($r = 0.633$) and both kriging maps indicated a decrease in diversity from the centre toward southern and south-western parts of the continent (Fig. 3). For the two groups, high species richness is found in northern South America and in the south-eastern coast of Brazil, with gradients between the two zones. The Andean region has lower species richness, a pattern that is more marked for Falconiformes. These patterns are also reflected in the frequency distribution of species richness (Fig. 4), which are bimodal, specially for the Falconiformes.

The correlation between observed richness and expected richness under a bi-dimensional extension of Willig & Lyons' (1998) null model was very low for the two groups, with $r^2 = 0.046$ for Falconiformes and $r^2 = 0.018$ for Strigiformes. Excluding species whose geographical ranges extend beyond South America did not improve agreement between data and null model ($r^2 = 0.002$ for Falconiformes and $r^2 = 0.028$ for Strigiformes). In spite of bias caused by autocorrelation among quadrats (as distances between the 32 quadrats are smaller than the ranges defined by the semi-variograms; see Bini *et al.* 2000), observed Type I errors are much higher than 5% and, so, these results are strongly conservative. For the Falconiformes, there is a marked distinction between the two zones of the continent (northern and south-eastern South America vs. the Andean region) in the scatterplot relating observed richness and proportion of continental pool (Fig. 5).

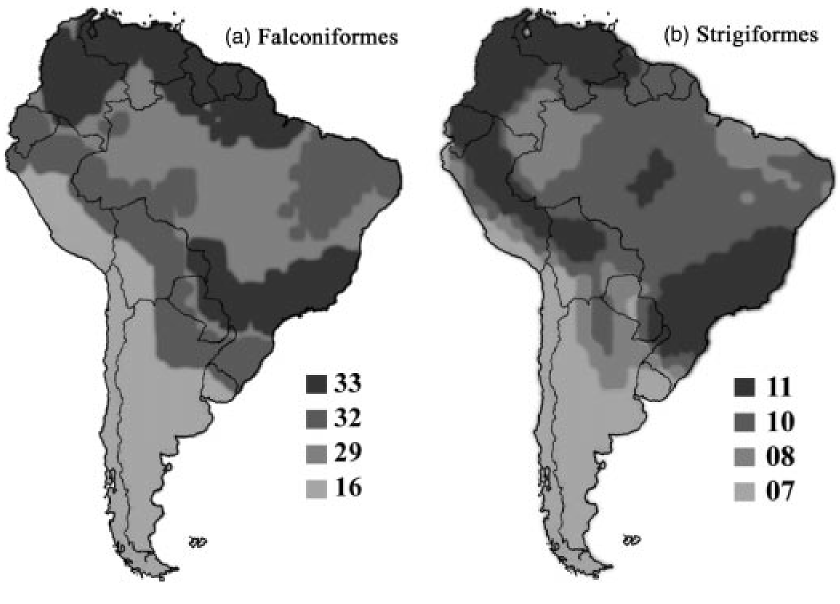

Figure 3 Interpolated kriging maps for species richness of (a) Falconiformes and (b) Strigiformes in South America.

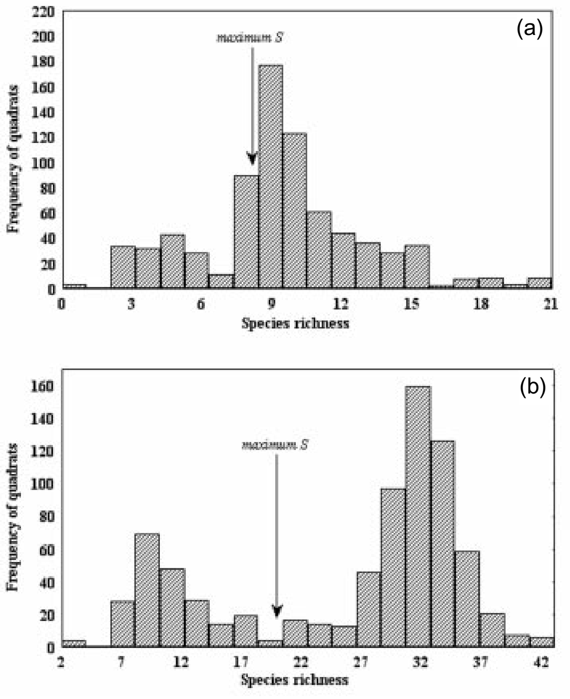

Figure 4 Frequency distribution of species richness in the 780 quadrats covering South America, for (a) Falconiformes and (b) Strigiformes. The arrows indicate maximum species richness by the null model, when *p*, *q*, *s* and *t* are equal to 0.5.

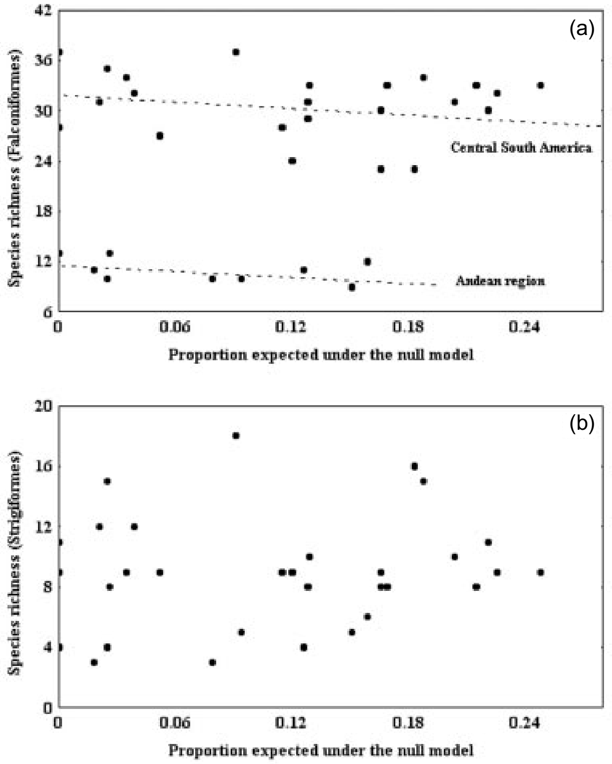

Figure 5 Relationship between observed species richness and proportion of continental pool (4pqst) expected under the null model, for (a) Falconiformes and (b) Strigiformes.

Interpolated surfaces were also obtained for the difference between observed and expected richness under the null model for the two groups, in such a way that is possible to map where observed richness departs from null expectation (Fig. 6). Errors in the estimation of the regional pool does not affect these differences in relative terms, only their relative magnitude. It is possible to observe that, in general, the null model underestimate the real richness across the continent (see also Fig. 4). For the Falconiformes, richness is estimated well only for the transition area situated between Central and Andean regions of South America. In the central portion of the continent, real diversity is higher than predicted, while in the Andean region the opposite occurs. Because there is a bi-dimensional gradient in the null model from the centre toward the periphery of the continent, in all directions, richness tends to be overestimated at the extremes of the continent, specially in the southern portion. For the Strigiformes, the overall area with a small bias in estimation is much larger than for the Falconiformes.

The effect of biome on species richness was also significant for the two groups analysed here. It was observed that the effect of habitat explained 77.5% and 59.3% of variation in richness in Falconiformes and Strigiformes, respectively. However, these values are probably overestimated because biomes are patterned in geographical space and so also possesses an strong spatial component, being also constrained by continent shape and topography. But even after introducing a third-order polynomial expansion of geographical coordinates of quadrats as covariates in the anova model, to control for these spatial patterns, the effect of biome type remains significant at the 5% level in both cases.

DISCUSSION

The species richness in the two groups of birds of prey analysed here are strongly patterned over geographical space, although these patterns cannot be expressed as simple latitudinal gradient. The patterns cannot be interpreted as a simple function of the continental edges and overlap of randomly allocated geographical ranges, as predicted by mid-domain effect, since correspondence between observed and expected richness under a bi-dimensional null model is very low. This contrasts with previous findings, specially for mammals, that detected a relatively high correspondence between expected and observed richness, although in many papers only latitudinal

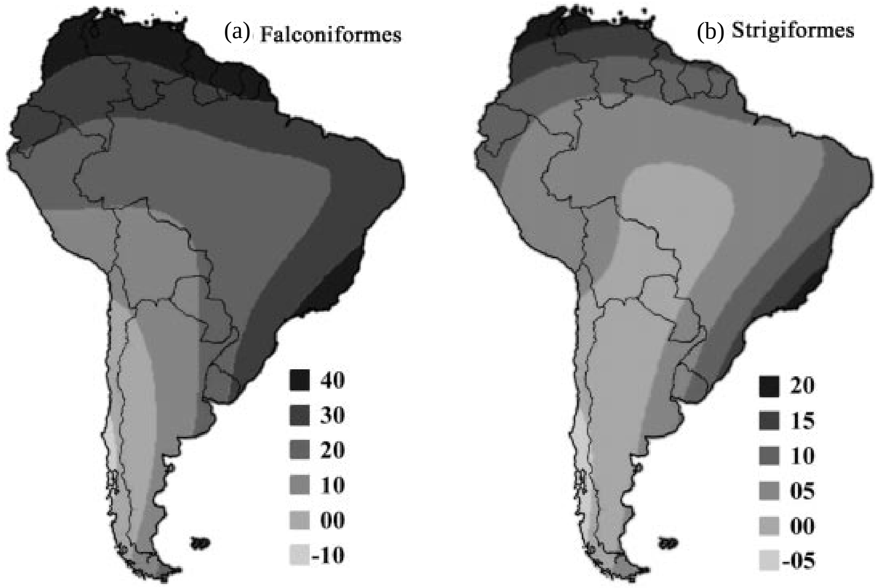

Figure 6 Maps showing differences between observed richness and expected richness under the null model for (a) Falconiformes and (b) Strigiformes.

patterns were analysed (see Willig & Lyons 1998; Lyons & Willig 1997, 1999). However, as pointed out by Bokma & Mönkkönen (2000) and Bokma *et al.* (2001), when the configuration of a landmass in a bi-dimensional space is incorporated into the null models, the results can be dramatically different from previous simulations that considered only latitudinal effects and, in this way, stochastic mechanisms usually cannot account for gradients in species richness (but see Jetz & Rahbek 2001).

The null model used in this paper is a bi-dimensional extension of the analytical model proposed by Willig & Lyons (1998) but, as in any mid-domain model, model also it must take into account the geometry of the area under analysis (i.e. South American continent). Since proportions *p, q, s* and *t* were calculated considering the closest continental edge, the high levels of species richness lies approximately in the middle of the landmass. Adding North and Central America will not affect our results because the analytical null model we used here is based on immediate boundaries of the continent, and the area constriction in Central America will cause a double-peak shift in North and South America (compare our Fig. 1b) with surface shown in Fig. 2 of Bokma *et al.* 2001). Other bi-dimensional null models, such as the 'evolutionary' model of Bokma *et al.* (2001) and the 'spreading dye' model of Jetz & Rahbek's (2001), also predict similar patterns of expected species richness. There is also discussion about how realistic all these null models are, so that, at the present time, it is difficult to choose between them (Colwell & Lees 2000b; Koleff & Gaston 2001).

We believe that using more complex null models based on simulation of geographical ranges in a bi-dimensional space will not qualitatively change our conclusions. The midpoints of geographical ranges used for both groups are widely distributed in South America, and many species of these groups can be found in the extremes of the continent, indicating ecological tolerance across all regions (Koleff & Gaston 2001). Despite difficulties in a clear quantitative evaluation of the robustness of the Willig & Lyons (1998) null model to violations of its assumptions, they seem nonetheless not to be serious. More importantly, using only species endemic to South America did not improve agreement between the data and the null model. In fact, when we removed the species that fall outside South America, the correlation between observed and expected richness is reduced, especially for Falconiformes. This can partially explained by leaving in the model only species with relatively small geographical ranges, situated in Andes and Atlantic forest. This slight change tends to support the idea that the mid-domain effect is more evident for species with relatively large geographical ranges and will consequently be more strongly affected by geometric constraints (Lees *et al.* 1999; Jetz & Rahbek 2001). Unfortunately, our data do not permit a clear quantitative test of this idea, due to the relatively low number of species.

As a consequence, the higher relative differences between observed and expected richness by mid-domain null models will tend to occur always at the edges of the South American continent, as in this study. For the two groups of birds of prey, remarkable departures from the null model occur on the south-eastern coast of South America (i.e., the Atlantic rain forest) and in northern South America, close to Central American (the Amazonian rain forest), in which richness is higher than expected. On the other hand, in the extreme south of the continent (south-western Anden region), richness tends to be lower than expected. These patterns suggest effects of habitat variation in the spatial variation of species richness at continental scales.

Species richness of the two groups analysed here, especially the Falconiformes, seems to be strongly affected by biome type and shape. Also, the Andes affect the shape of the geographical ranges in South America and, consequently, bias the patterns of range overlap by chance alone, creating distinct biogeographical zones (Rapoport 1975; Graves 1988; Rahbek 1997; Ruggiero & Lawton 1998; Rahbek & Graves 2000, 2001). Thiollay (1996) and Rahbek (1997) showed particularly for raptors that altitude and topography have specific effects on abundance and richness, requiring adaptations for extreme environmental conditions. Similar patterns of species richness variation in South America were also found by Ruggiero *et al.* (1998), analysing areographical patterns of mammalian species in a bi-dimensional context. So, as habitat type and topographical features constraint geographical range for some species, the mid-domain effect would not be only tested at the continental scale, but within large-scale habitat types or biographic zones, that may be distinct by accumulation of historical events of speciation and extinction. In this case, further investigations must determinate if there would be a partition in the explanatory factors associated with diversity patterns, at different geographical scales, combining both deterministic ecological and historical mechanisms ('between' habitats or biogeographical zones) and stochastic overlap of geometrically constrained ranges ('within' them).

In accordance with these previous results, biome type explained a large amount of variation in richness in Falconiformes and Strigiformes. However, these high values cannot be interpreted alone because biome variation, as used in this paper, is in fact a surrogate variable that is affected by many abiotic factors (i.e. temperature, moisture, altitude and topography, energy available, and so on) (Pagel *et al.* 1991; see also Blackburn & Gaston 1996a). Indeed, most studies explaining latitudinal gradients are based on correlation between species richness and variation in other biotic or abiotic factors, and they usually lead only to the best descriptors of the patterns, but not necessarily indicate primary causes because of the correlation among them (multicolinearity) (Rohde 1992; Rahbek & Graves 2000, 2001; Bokma *et al.* 2001). It is important to note that this collinearity problem is valid even when a mid-domain model is corroborated by the data, because if habitat types have a strong influence on diversity but at the same time are constrained in size and shape by the physical boundaries of the continent, a random overlap of geographical range would be equivocally proposed as the most parsimonious explanation for the observed pattern (Bradford Hawkins, personal communication).

In addition, Rahbek & Graves (2000, 2001) recently showed that using large grids to analyse diversity (as in Blackburn & Gaston 1996a; Blackburn & Gaston 1996b; and many papers that follow them) obscures the finer structure of spatial patterns, reducing the statistical power of analyses. We followed the recommendation of Rahbek & Graves (2000) who pointed out that, although there would be no single correct scale for macroecological analyses, finer scales should be preferred. When dealing with finer scales, however, autocorrelation in species richness becomes stronger, increasing Type I error in correlation and regression analyses. Although in this paper no 'significant' correlations appeared (so our results are in fact conservative in respect to spatial autocorrelation), the method proposed by Bini *et al.* (2000) can be used to overcome this autocorrelation problem (see Jetz & Rahbek 2001).

Another important point of difference between observed and expected richness seems to be in model calibration using continental species pool. Although these S-values do not change the fit of the null model to real data, the scale of difference maps are, of course, strongly influenced by this choice. But in the two groups analysed here, the observed richness is higher than expected throughout large extents of the landmass, indicating that range overlap is higher than expected by chance in many regions of the continent. Koleff & Gaston (2001) recently found that observed turnover levels (i.e. beta diversity) were also higher than those expected from different mid-domain null models for two groups of South American birds (parrots and woodpeckers). Once again, this could be explained by aggregation of species' geographical ranges throughout the continent caused by suitable environments.

As pointed out by Flather (1996) and Böhning-Gaese (1997), avian species richness may be strongly influenced by habitat diversity and land-use patterns, although these effects seem to be clear at relatively small (local) spatial scales. However, at large spatial scales, as analysed here, correlations between abiotic factors, such as topography, available energy and temperature, also affect biome diversity, area and shape in such a way that it may be difficult to chose between alternative hypotheses explaining variation in species richness or diversity (Rohde 1992; Rahbek 1997; Hillebrand & Azovsky 2001). Blackburn & Gaston (1996b), Ruggiero & Lawton (1998) and Rahbek & Graves (2000) showed that geographical extends of birds and, consequently, patterns of range overlap creating large-scale diversity estimates, are strongly correlated with biome size and shape variation in the South American continent, thus confirming the departures from the null model observed in this paper.

Variation in species richness in South American Falconiformes and Strigiformes is strongly patterned in geographical space, but it does not follow a simple null model based on random allocation of species ranges within continental boundaries. Although it is difficult to find a primary explanation for the patterns observed, biome variation seems to be associated with departures from the null model. Further tests of these effects and possible mid-domain effects within biomes are necessary. The evaluation of how these departures occur is a crucial step toward understanding the ecological and evolutionary factors explaining variation in species richness at large geographical scales.

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