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# Local and regional species diversity in South American Falconiformes: a geostatistical approach

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**ABSTRACT.** The relationship between local and regional diversity in Falconiformes assemblages from South America was estimated. However, species richness was spatially patterned across the continent and this result can bias significance levels of regression analyses. To overcome this problem, we determined the minimum distance between localities that ensures stochastic independence of diversity estimates across space, using geostatistical analyses. Based on the range obtained by a variogram, we analyzed the relationship between local and regional diversity using three regions separated by more than 4800 km. To increase robustness of results, we used 30 different combinations of three regions. Most linear regression slopes between local and regional diversity are significant, but none of the quadratic terms added to test local saturation was significant. This indicates that local assemblages of Falconiformes are unsaturated. Overall, this result indicates the importance of regional and historical processes in the determination of species richness at local scales.

**Key words:** Falconiformes, regional and local diversity relationship, geostatistics.

**RESUMO. Diversidade local e regional de espécies de Falconiformes da América do Sul: uma abordagem geoestatística.** A relação entre a diversidade local e regional em assembléias de Falconiformes da América do Sul foi estimada. Entretanto, a riqueza da espécie apresentou autocorrelação espacial ao longo do continente e este resultado pode enviesar os níveis de significância das análises de regressão. Para superar este problema, determinou-se a distância mínima entre localidades que garantiria a independência estocástica das estimativas da diversidade ao longo do espaço. Para tanto análises geoestatísticas foram utilizadas. Com base na amplitude indicada pelo variograma, analisamos a relação entre a diversidade local e regional usando três regiões separadas por mais do que 4.800km. Para aumentar a robustez dos resultados, foram analisadas 30 combinações diferentes de três regiões. A maior parte dos coeficientes na regressão linear entre a diversidade local e regional foi significativa, mas somente dois dos termos quadráticos adicionados para testar a saturação local foram significativos. Isto indica que as assembléias de Falconiformes, numa escala local, não estão saturadas. Em geral, este resultado indica a importância dos processos históricos e regionais sobre a determinação da riqueza de espécies em escala local.

**Palavras-chave:** Falconiformes, relação entre diversidade regional e local, geoestatística.

Local species richness is defined as the number of species that can be measured on a spatial scale small enough so that all the species could encounter each other within ecological time, and so possibly interact (Srivastava, 1999). This is a key variable in ecological communities analysis and many authors (e.g. Rhode, 1992; Ricklefs and Schluter, 1993; Rosenzweig, 1995) tried and are still trying to find causal mechanisms that explain its spatial or temporal variation.

Species richness on local scales could be limited by either ecological (e.g. upper limits to niche packing, minimum viable population) or evolutionary causes (e.g. rates of speciation, fixation rate of mutations which allow new habitats to be invaded) (Srivastava, 1999). An efficient way to assess the relative roles of local-ecological and regional-evolutionary processes in determining local patterns of species richness is to regress local on regional estimates of species richness (Cornell, 1993), despite some methodological problems (Cresswell *et al.*, 1995; Caley, 1997; Caley e Schluter, 1997). If a linear relationship between these two components of diversity is detected, the local communities are said to be unsaturated with species (Cornell, 1985; Cornell and Lawton, 1992; Cornell, 1993). In this case, the influence of regional and historical processes (e.g., speciation, regional extinction, dispersion) can be used to explain local community structure (Ricklefs, 1987). In contrast, independence of local and regional richness or curvilinear relationships indicate that local communities are saturated (Terborgh and Faaborg, 1980), in such a way that local interactions between species and the physical environment could be invoked to explain local community structure (Ricklefs, 1987).

It is important to note, however, that a linear pattern (also called "proportional sampling") does not necessarily mean that the local community is noninteractive (Caley and Schluter, 1997; Griffiths, 1999). According to Cornell (1993), all that proportional sampling indicates is that regardless of the nature of any local interactions that may be occurring, they are not sufficient to limit local diversity. On the other hand, saturating curves can be a result of sampling artefacts (Griffiths, 1999)

Caley and Schluter (1998) recently emphasized that species-area plots (an alternative method suggested by Westoby (1998) to study saturation of local species diversity), as well as local-regional species richness regression, are constrained by the small number of independent biogeographic regions available in most studies. In this way, both methods have low statistical power to detect saturation due to the low number of degrees of freedom (Srivastava, 1999). On the other hand, those tests of saturation that include multiple values of species richness from the same region will suffer from pseudoreplication (Hurlbert, 1984; Legendre, 1993).

In this paper, we examine the relationship between local and regional species richness of Falconiformes from South America, showing how it is possible to study local and regional diversity relationships using more than one region per continent. This can be done by applying geostatistical techniques to determine the minimum geographic distance between regions that ensures that observations are spatially independent for subsequent regression analyses (Bini *et al.*, 2000).

## Material and methods

**Data.** The 80 species of South American Falconiformes (Dunning, 1987; Sibley and Monroe, 1990; Sick, 1997) were analyzed by mapping their geographical ranges (their extent of occurrence - Gaston, 1991, 1996). These distribution maps were redrawn on a standardized grid map of South America with 780 quadrats, 135 km on a side, using polyconic projection. For each quadrat in the grid, the number of species occupying each quadrat was recorded as an estimate of local diversity (grid diversity).

**Data analysis.** A typical problem in assessing the relationship between local and regional diversity is gathering independent observations, and some authors have avoided this problem by using a single region per continent (e.g., Caley and Schluter, 1997). Although this approach is correct, it may provide too few degrees of freedom for analyses. We tried to overcome this problem by using spatial statistics to define the minimum geographical distance between localities that ensures independence of diversity estimates (Bini *et al.*, 2000).

First, a variogram was used to model the spatial variation of species richness across the continent. Variograms represent the average degree of dissimilarity between sites (grids, in this case) as a function of their separation distance (Cressie, 1989; Legendre and Fortin, 1989). The semivariance ($\hat{\gamma}$) is estimated by:

$$\hat{\gamma}(h)=\frac{1}{2N(h)}\sum_{i=1}^{N(h)}\left[Z(x_i+h)-Z(x_i)^2\right] ,$$

where $\hat{\gamma}(h)$ is the estimated semivariance value for lag $h$, $N(h)$ is the number of pairs of points separated by $h$ and $Z$ is the value of the variable at point $x_i$. When the semivariance is plotted against sampling intervals or lag ($h$), the resulting graph is known as semivariogram, or variogram.

In this study, the omnidirectional variogram, where values of $\hat{\gamma}(h)$ are independent of direction (isotropy assumption), was computed using the US Environmental Protection Agency program "Geo-EAS". The adjustment of a model (theoretical variogram) to a set of points on the experimental variogram supplied some important parameters (Maurer, 1994; Rossi *et al.*, 1992): i) the range of autocorrelation, that gives the distance within which the samples remain autocorrelated; ii) the sill ($C_1$), that indicates the maximum variability due to the structure (the value, on the ordinate of the variogram, where the semi-variance is constant) and; iii) the nugget effect ($C_0$), that denotes the unresolved small-scale variability and sampling error (the value of the semi-variance at spatial distance equal to zero). So, the ratio $C_0/C_0+C_1$ gives the proportion of the unresolved small-scale variability to the total variability ($C_0+C_1$).

Once the geographic distance that insures statistical independence of diversity estimates was established according to the estimated range of autocorrelation, we defined by triangulation a sampling grid to locate the center of each region. We emphasize that the centers of these regions were separated by a distance larger than the range defined above. Following Caley and Schluter (1997), local diversity was estimated for a single quadrat (135 X 135 km) in the grid at the center of each of the defined regions. Region size was defined arbitrarily as 16.4 x $10^4$ $km^2$, corresponding to 9 quadrats around the localities defined as the center of each region. Previous work (Bini *et al.*, 2000) indicated that few qualitative differences are detected by increasing region size. Anyway, this increase would generate autocorrelation because larger regions will become gradually closer in geographic space. Westoby (1998) also criticized the procedure used by Caley and Schluter (1997) due to the use of too large areas to represent local species richness and, in this way, making it much more difficult to detect saturation. However, as indicated by Caley and Schluter (1998), the use of "larger-than-typical localities" (sensu Cornell, 1985) is a simple way to minimize the impact of pseudosaturation (a bias in estimating local diversity due to sampling rare species).

Regional species richness was defined as the total number of species found in each region minus the number of species found exclusively in the center quadrat of each region. The local species diversity was defined as the number of species found in the quadrat located at the center of the region (the target locality). This procedure was adopted because significance levels of regressions of local on regional diversity are biased if those species that are endemic to target localities are summed to calculate regional diversity (Cresswell *et al.,* 1995; Caley, 1997). Local diversity was then regressed on the regional diversity and, in an attempt to detect local saturation, curvilinearity in the relationships was evaluated by adding to the linear model a second-order polynomial term (Caley and Schluter, 1997).

## Results

Variographic analysis of total grid data indicated that local diversity is strongly spatially correlated (Figure 1). The unresolved small-scale variability (the nugget effect = 5) represented approximately 1 % of the total variability (sill = 450), and the range of spatial autocorrelation was established to be around 4,800 km. A three-dimensional scatterplot of local diversity also indicates a long-range gradient, with low diversity in southern regions of the continent (Figure 2).

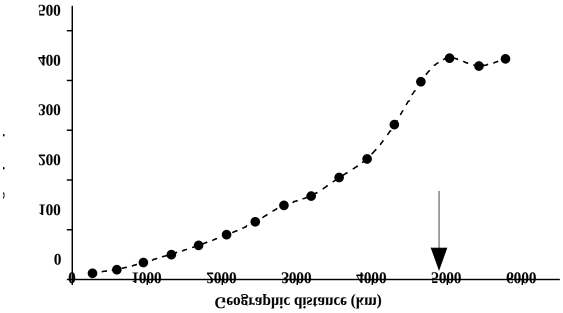

**Figure 1.** Experimental semi-variogram for species richness of Falconiformes in South America

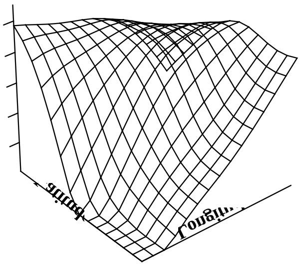

**Figure 2.** Distance Weight Least Square 3-D map of species richness of Falconiformes variation across South America

Using the range parameter suggested by the overall variogram, the minimum separation distance within which the grid samples are no longer autocorrelated was 4,800 km. In other words, the values at pairs of locations this distance apart are no more similar than expected for randomly observed pairs. This value was then used as the minimum geographical distance between the centers of regions. In this way, regression estimates can be considered spatially independent (Maurer, 1994).

However, because of the large range, which in turn is related to the slowness of the diversity gradient, only three points can be used as centers of the regions with South America (Figure 3). Regressions then were conducted with only three points, which makes in return to the problems discussed by Caley and Schluter (1997, 1998). In an attempt to minimize the problem of low statistical power, we repeated the procedure 30 times, assigning at each time a different combination of three regions separated by more than 4,800 km. Due to low degrees of freedom it is impossible to estimate the statistical significance of regression coefficients. Anyway, only nine quadratic slopes, out of 30 regression analyses, were negative, which could indicate saturation. It is interesting to note, however, that linear terms (standardized coefficients) were significantly larger than those negative quadratic terms (standardized coefficients multiplied by -1) (paired $t$ test = 112.9; $n$ = 9; $P$ = 0.000).

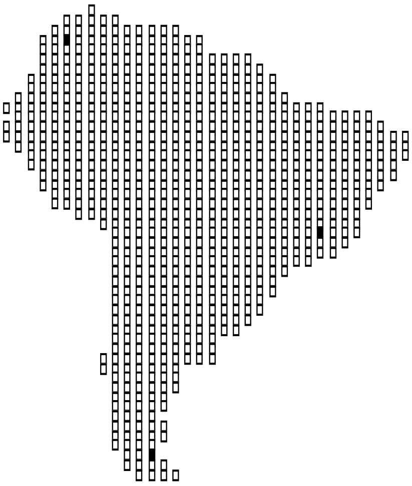

**Figure 3.** One example of sampling grid (filled squares) defined by the variographic analysis, used to define region centers (target localities) distant more than 4800 km apart

## Discussion

Spatial patterns of diversity of Falconiformes in South America indicate long distance gradients of diversity. This pattern is in accordance with the well-known gradients in species diversity for many different kinds of organisms (Rhode, 1992; Rosenzweig, 1995). Despite the extensive discussion of causal evolutionary and ecological mechanisms leading to these gradients, the main implication of the phenomena for this work is that the gradients make it much more difficult to test the relative balance between regional and local processes structuring local communities within a single large continental area.

The method proposed by Bini *et al.* (2000) to increase the power of local versus regional regressions in a single continuous area is based on the application of geostatistical methods (variograms) to assess a minimum geographic distance between regions that ensures that data points are independent for regression analyses. In principle, this overcame the problem of using only one region per continent, which obviously decreases the number of degrees of freedom for analyses and the ability to detect significant linear, and especially curvilinear, relationships between local and regional diversity (Westoby, 1998). However, as Bini *et al.* (2000) indicated, the validity of their method depends on the establishment of a well-defined range that permits identification of the minimum distance between the edges of the regions. Thus, the application of the proposed method to the Falconiformes data set introduced a new difficulty due to the shape of the large spatial patterns in diversity. The almost linear variogram found in this study does not include a clear sill, and in this case the semivariance seems to stabilize only at a very large geographical distance (more than 4,500 km). Consequently, a few independent regions can be used for regression analyses. Although this is a problem for the statistical analyses and for the discrimination between alternative hypotheses explaining the relationship between local and regional diversity, it is coherent with the large-scale spatial patterns of diversity found in this group.

The linear relationships found do not indicate that local communities are noninteractive, only that local interactions between species are not strong enough to constrain local diversity (Caley and Schluter, 1997). This low effect can be explained both by ecological processes, such as character displacements and other mechanisms that permit local coexistence, or by methodological bias related to definitions of local and regional scales (Srivastava, 1999). At the present time, it is difficult to test between the two alternative explanations for the proportional sampling found in the data. However, it seems to be most parsimonious to conclude that there is a general linear relationship between local and regional diversity, as predicted by the regional enrichment model (Cornell, 1985; Ricklefs, 1987). Indeed, evidence of local saturation occurs when local and regional species richness are unrelated or when a curvilinear model (concave down) best describes the relationship between these two quantities (Cornell and Lawton, 1992). Despite the interesting theoretical aspects involving saturation in communities, few studies have reported local saturation in vertebrate assemblages (Cornell, 1993; Caley and Schluter, 1997). Our results also indicate that Falconiformes assemblages in South America are also not saturated, suggesting that large-scale spatial and historical processes, such as colonization, speciation and extinction, are very important in determining local diversity in these organisms. This pattern suggests that, in some instances, questions regarding the abundance and richness within local assemblages of these organisms could also address large scale temporal and spatial processes, beyond traditional considerations involving niche metrics related to body size variation, prey size and habitat type (Schoener, 1984).

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