Research

Ecography 32: 226–236, 2009
doi: 10.1111/j.1600-0587.2008.05502.x

Subject Editor: Jens-Christian Svenning. Accepted 23 June 2008

Environmental drivers of beta-diversity patterns in New-World birds and mammals

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Current macroecological research places great emphasis on patterns of species richness (alpha diversity) and the underlying ecological and evolutionary processes involved in their origin and maintenance. However, few studies dealing with continental scales have addressed dissimilarities in species composition among areas (beta diversity). Using data for the occurrence of 3836 bird and 1641 mammal species in 4220 cells covering the New World, we assessed whether broad-scale macroecological patterns in beta diversity are related to dissimilarities in environmental variables and biotic units. We employed spatial regression and tree regression to model beta diversity. Difference in altitude was the best predictor of beta diversity. Accordingly, the highest beta diversity values were found in mountainous areas, particularly in the Andes, Central America and western North America. Explanatory variables related to transitions between biotic units (biome, ecoregion) were relatively unimportant. Areas that differ in altitude from their surroundings harbor different sets of species, and this may reflect either species adaptation to particular environmental conditions by range shifts, or species divergence by vicariance, or both.

Early ecologists recognized that biological diversity in an area can be decomposed into two components. The first component relates to the number of species found in a single site or habitat. The second component concerns the change in species composition among sites, habitats or gradients. Whittaker (1960, 1972) termed the first component alpha diversity, and the second component beta diversity. He termed gamma diversity the total diversity of all sites or habitats, and proposed that gamma = alpha × beta. This simple relationship has been applied in a number of studies, particularly those dealing with differences among habitats or small-scale gradients (Koleff et al. 2003, Magurran 2004). Despite the wide use of the formula proposed by Whittaker (1960, 1972), many other formulas and even approaches have been suggested (Harrison et al. 1992, Koleff et al. 2003, Magurran 2004). For instance, beta diversity can be quantified as dissimilarities among sites (Koch 1957, Whittaker 1972, Koleff et al. 2003). Also, if a species-accumulation curve is constructed using nested subsamples (Crist and Veech 2006) and linearized by a log or a log-log transformation, the slope of the line adjusted to the data can be used as a measure of beta diversity (Rodríguez and Arita 2004). Thus, Diniz-Filho et al. (2004) used the equivalent z-parameter of the power function $S = cA^z$ as a measure of beta diversity among nested sets of quadrats (see also Lennon et al. 2001). Interest in beta diversity has resurged in the last 10 yr, stimulated in part by the popularization of additive partitioning (Veech and Crist 2007).

Although most of the literature treats different measures of beta diversity as synonyms, this is not always the case. For instance, Crist and Veech (2006) showed that the slope of a species-accumulation curve constructed using nested or non-nested areas results in different measures of beta diversity. Koleff et al. (2003) compiled 18 formulas used in beta diversity studies, and showed that they respond differently to variation in their matching components, and that some of them are oversensitive to differences in species richness among samples. When using dissimilarities to quantify beta diversity among samples, one may opt to use a multiple-site approach where a single value is obtained from all the samples in the comparison (Diserud and Ødegaard 2007, Baselga et al. 2007). In contrast, a pair-wise approach produces a single beta diversity value for each sample, consisting of the mean dissimilarities from a focal cell and all the remaining cells. Although usually treated as synonyms, the multiple-site approach measures beta diversity using all information on differences among samples, and is directly related to the multiplicative formulas proposed by Whittaker (1960). In contrast, the pair-wise approach quantifies the difference between a focal sample and the remaining samples.

At broad macroecological scales, much emphasis has been given to patterns of species richness and the associated

ecological and evolutionary processes underlying their origin and maintenance (Hawkins et al. 2003, Currie et al. 2004, Kark et al. 2007, Qian et al. 2007, Rangel et al. 2007). These macroecological studies usually did not take into account dissimilarities among assemblages at a given spatial scale. However, diversity within (alpha) and among (beta) areas seems to be intrinsically associated, and some mechanisms that are usually associated with richness gradients, especially those related to niche dynamics over ecological and evolutionary time spans, are actually driven by changes in species composition among areas (Qian et al. 2005, Qian and Ricklefs 2007). For example, Stevens (1989), in his classical paper on Rapoport's rule, suggested that increasing species turnover towards tropical regions, associated with the decrease in geographical range size as a consequence of increasing habitat specialization, could explain the diversity gradients. Although the association between latitudinal gradients in geographical range size (Rapoport's rule) and richness has been widely discussed and questioned (Gaston et al. 1998, Hawkins and Diniz-Filho 2006), packing mechanisms (such as habitat specialization and niche-breath reduction) may generate high alpha diversity on a large scale, as a result of increased beta diversity at smaller scales (Rodríguez and Arita 2004).

A few macroecological studies have treated broad-scale patterns of beta diversity. Mourelle and Ezcurra (1997) evaluated patterns of beta diversity of cacti in Argentina, and found that variation among one-degree cells was highest in the northwest part of the country, an area with highly variable topography and many transitions among biogeographical provinces. Lennon et al. (2001) analyzed patterns in beta diversity in British birds, showed how these patterns change with the spatial scale of the analysis (i.e. grain size), and discussed the implications of these findings for conservation biology. More recently, Qian and Ricklefs (2007) evaluated broad-scale patterns of beta diversity of native vascular-plant communities in latitudinal bands of North America, concluding that a north-south gradient in the magnitude of beta diversity exists. They also showed that geographical and environmental distances explained about the same amount of variation in beta-diversity gradients, and there has indeed been a recent trend to associate these two sources, respectively, with neutral (dispersion and historical events) and niche-based adaptive processes. McKnight et al. (2007) mapped beta diversity of birds, mammals and amphibians in the Western Hemisphere, and found that congruence in regions of high beta diversity among the groups depended on the region studied, being higher in the Neotropical than in the Nearctic realm.

Broad-scale studies usually do not evaluate continuous patterns of variation in beta diversity at geographical scales (but see Mourelle and Ezcurra 1997, Rodríguez and Arita 2004, van Rensburg et al. 2004, Gaston et al. 2007, McKnight et al. 2007). Instead, these studies usually focus on the comparison of spatially distant areas, ecoregions and latitudinal bands (Harrison et al. 1992, Blackburn and Gaston 1996, Willig and Gannon 1997, Qian et al. 2005, Wittmann et al. 2006, Qian and Ricklefs 2007, Veech and Crist 2007). Also, most beta-diversity studies, irrespective of the spatial scale concerned, have focused on documenting patterns, and only rarely have they explicitly attempted to evaluate ecological and evolutionary factors generating beta diversity (but see Mourelle and Ezcurra 1997, van Rensburg et al. 2004, Qian et al. 2005, Harborne et al. 2006).

Beta diversity is generated broadly by geographical distance and environmental differences (Cody 1986, Condit et al. 2002, Tuomisto et al. 2003, Legendre et al. 2005, Tuomisto and Ruokolainen 2006, Steinitz et al. 2006). Restrictions on dispersal may produce autocorrelated distributions of individuals of each species. Accordingly, distant areas will contain different sets of species. This hypothesis assumes that species are able to survive and reproduce irrespective of habitat conditions, and that dispersal limitation is the key factor generating dissimilarities in species composition among areas. Accordingly, we would expect that taxa differing in dispersal abilities would differ in beta diversity (Steinitz et al. 2006). In contrast, traditional ecological theory predicts that species are limited in space by their niche requirements. Areas with contrasting environmental conditions would harbor different sets of species (Cody 1986).

We evaluated biotic and abiotic predictors of broad-scale macroecological patterns in beta diversity of New World birds and mammals. We mapped beta diversity for each 1° by 1° cell using the pair-wise approach, wherein each focal cell is compared to its first-order adjacent cells. Our measure of beta diversity thus quantifies how different the focal cell is in relation to its adjacent cells. We hypothesize that beta diversity is generated by differences in environmental conditions of areas. Using two regression approaches, we selected abiotic and biotic predictors that best predicted the distinctiveness in species composition of a cell in relation to its adjacent cells.

We used a beta-diversity index developed by Lennon et al. (2001) that allows evaluation of patterns of beta diversity independently of species-richness gradients. Because our beta-diversity measure quantifies mean dissimilarities of a focal cell in relation to its neighborhood cells, we used the differences in environmental variables between the focal cell and its adjacent cells as predictors. This approach has been rarely used to model beta diversity.

Materials and methods

Data

For the analysis, we used the digitized bird (Ridgely et al. 2005) and mammal (Patterson et al. 2005) databases for 3836 bird species and 1641 mammal species, available at <www.natureserve.org>. These databases have been extensively used in broad-scale diversity and macroecological analyses (Hawkins and Diniz-Filho 2006, Hawkins et al. 2007a, b, Rangel et al. 2007, Diniz-Filho et al. 2008; see also Orme et al. 2005 and subsequent papers using the global bird-distribution dataset). The databases were processed using ESRI ArcView 3.1 scripts to record each species' presence, as defined by its breeding range, in the 1° by 1° cell grid ($m = 4220$) covering the New World. Cells with $<50\%$ land area, and small islands were excluded from the grid. We then constructed a presence/absence matrix for the entire New World, to allow calculating different metrics for the beta diversity of each

cell using functions written in the R environment (R Development Core Team 2007) (see below).

Environmental predictors of beta diversity

Beta diversity has been interpreted in many ways, and as a consequence many formulas and approaches have been suggested (Koleff et al. 2003, Legendre et al. 2005, Tuomisto and Ruokolainen 2006). In our study, beta diversity is measured and interpreted as distinctiveness. This usage has been employed in conservation studies aimed toward designing representative networks of protected areas (Wiersma and Urban 2005). In the present study, beta diversity in each squared cell measures how different this cell is, in terms of species composition, from the adjacent cells. Accordingly, we can expect that its distinctiveness will be due to differences in environmental conditions between the focal and adjacent cells. We thus modeled beta diversity in a given cell in relation to the distinctiveness of the cell in terms of environmental predictors. The distinctiveness of an environmental predictor has only rarely been used to model beta diversity (Mourelle and Ezcurra 1997, Gaston et al. 2007). In case of important relationships between beta diversity and distinctiveness of environmental predictors, the direct interpretation is that species are adapted to their environment, and therefore change in the environment is accompanied by change in species composition. An indirect relationship mediated by species occupancy, which was not evaluated here, was reported by Gaston et al. (2007) between beta diversity and mean environmental predictors of the focal grid cell. The authors argued that abundant resources would allow the occurrence of many species with large ranges, which in turn would decrease beta diversity (see also Cody 1986).

For each of the following seven environmental factors, which are commonly used in the analyses of broad-scale diversity patterns, we obtained the mean differences of the values in the focal cell from all of its adjacent cells. For clarity, in the remaining text we refer to each of these environmental predictors as its name plus the suffix ''.dif'' to indicate that differences, and not the original values of the variable, are being used: 1) altitude, 2) temperature 3) precipitation, 4) humidity, 5) net primary productivity (NPP), 6) potential evapo-transpiration (PET), and 7) actual evapo-transpiration (AET) (see New et al. 1999, Willmott and Kenji 2001, Hawkins et al. 2007a, Rangel et al. 2007, for detailed definitions of variables and sources).

In addition to environmental variables, beta diversity of birds and mammals may be affected by biotic differences among the areas where they live. Therefore, we should expect high beta diversity among adjacent cells located in different ecoregions or biomes (Williams 1996, van Rensburg et al. 2004, Kark et al. 2007), although a test using birds, mammals and trees in the United States and Canada did not support this expectation (McDonald et al. 2005). We investigated this expectation using the classification system for the Terrestrial Ecoregions of the world, available at: <http://www.worldwildlife.org/science/data/item1872.html> (Olson et al. 2001). The system is composed of three types of variables: realms, biomes and ecoregions (Olson et al. 2001). A fourth variable indicates habitat polygons within each ecoregion (available in the database). For each of the four variable types, we calculated the Jaccard distance index between the focal cell and all the first-order adjacent cells. Cells in the interior of biotic units should receive low values of distance, while those cells in transition zones should receive high values. Thus, in addition to the seven abiotic difference variables, we considered as predictors the mean Jaccard distance based on 8) realms (realms.jac), 9) biomes (biomes.jac), 10) ecoregions (ecoregions.jac), and 11) polygons (polygons.jac).

Before modeling, we analyzed the multicollinearity structure among predictors using the variance inflation factor (VIF). Based on this criterion, we found high VIFs for altitude.dif and temperature.dif (see correlations in Supplementary material, Table S1). However, after deleting temperature.dif, all VIF values became lower than 5, much lower than the critical heuristic value of 10. Thus, our final analyses were performed using 6 climatic variables (i.e. their pairwise differences) and 4 variables expressing differences among biotic units, as predictors.

Measuring beta diversity in grid systems

Since the pioneering work of Whittaker (1960), dozens of indices to measure beta diversity using presence-absence data have been proposed. Koleff et al. (2003) reviewed 60 publications dealing with the subject, and compiled 24 formulas. Because some formulas are re-expressions or equivalent forms of others, they listed 18 measures of beta diversity. We initially considered three measures of beta diversity listed by Koleff et al. (2003). The first measure was the Sørensen dissimilarity index:

$$\beta_{sor} = 1 - \frac{2a}{2a + b + c}$$

where a = number of species in both cells, b = number of species exclusive to the focal cell, and c = number of species exclusive to the adjacent cell. The Sørensen index (and its equivalent Jaccard, $\beta_j = 2^*\beta_{sor}/(1+\beta_{sor})$) is a popular choice in beta-diversity studies (Koleff et al. 2003, Magurran 2004). Despite its popularity, Lennon et al. (2001) pointed out that β_{sor} is very susceptible to differences in species richness between cells. For instance, Baselga et al. (2007) showed that the Sørensen dissimilarity index and its multiple-site version (Diserud and Ødegaard 2007) are not able to distinguish between nestedness and true differences in species composition among sites. Accordingly, Lennon et al. (2001) proposed two measures to distinguish beta diversity due to difference in species richness (β_{gl}) and due to difference in species composition (β_{sim}):

$$\beta_{gl} = \frac{2|b - c|}{2a + b + c},$$

$$\beta_{sim} = 1 - \frac{a}{a + \min(b, c)}.$$

We evaluated whether this was the case in our bird and mammal datasets. Indeed, the correlation between β_{gl} and the difference of β_{sor} and β_{sim} was extremely high for birds

($r = 0.95$) and mammals ($r = 0.98$). We compared the maps of beta diversity produced by β_{sor} and β_{sim} and found that they were quite similar. The few exceptions were large differences in some cells, usually in coastal areas, where β_{sor} produced relative values much higher than those produced by β_{sim}. Based on these two findings and on the recommendation of Lennon et al. (2001), we opted to use β_{sim} for all further analyses.

Beta diversity for each cell was quantified as the mean of the beta-diversity values between a focal cell and each of the eight adjacent cells. Increasing this distance of influence (i.e. calculating beta diversity for the 24 and 48 cells in second- and third-order adjacencies) did not qualitatively affect the patterns described here (results not shown). Means were obtained using fewer values for coastal cells. This approach was also used by Mourelle and Ezcurra (1997), Lennon et al. (2001) and Gaston et al. (2007) to study the beta diversity of Argentine cacti, British birds and the global avifauna respectively.

Statistical modeling of beta diversity

We evaluated the relationship between beta diversity and the 10 predictor variables using both regression tree (De'ath and Fabricius 2000) and multiple regression including spatial terms. Regression trees produce graphical binary trees that allow easy interpretation of main effects and interactions. On the other hand, multiple regression allows the inclusion of spatial terms to assess the influence of autocorrelation. We opted to use both methods, because they are complementary and can be used to assess the robustness of results from different analyses.

Regression tree

The regression tree method results in a binary tree, where a node represents a split of the data set according to an explanatory variable, and leaves represent the fitted value of the response variable. The analysis selects the explanatory variable that best partitions the response data into two homogenous groups. For continuous response data, this partition will be the one that maximizes the coefficient of determination (R^2). Each subgroup is then partitioned again, using the explanatory variable that best reduces the error within the two subgroups of data. The explanatory variable used in this second partition may be the same one used in the first split. This process of partitioning is known as growing the tree, and continues until the number of observations in each subgroup is considered small or when the increase in R^2 is small. This usually overlarge tree is then pruned to the size at which the splits significantly reduce the variability within subgroups. We used the package rpart (Therneau and Atkinson 2007) run under the R environment (R Development Core Team 2007) to obtain trees. Analyses were done using the ANOVA method and all default options, except that an overlarge tree was grown by setting the complexity parameter $cp = 0.001$.

We applied two criteria to prune the overlarge tree, and chose the one that resulted in the smallest tree. The first criterion was cross-validation, where a random subset of the data is used to grow the tree and predict the response in a second subset. We followed the recommendations of De'ath and Fabricius (2000) and used the 1-SE criterion to prune trees. This criterion consists of 1) selecting the tree that represents the smallest cross-validation error, 2) adding its respective 1-SE, and 3) obtaining the smallest tree with cross-validation error within the threshold: minimum cross-validation error plus its 1-SE. As cited above, the cross-validation procedure uses random subsets of the data. Accordingly, different error values will be obtained each time the cross-validation is run. The size of the tree selected by the 1-SE criterion may thus vary. We followed the suggestion of De'ath and Fabricius (2000) and computed the cross-validation 200 times, recording the size of the smallest tree within the 1-SE threshold. The most common size obtained in the 200 cross-validation was used to prune the final tree. Because our dataset is very large, a huge tree may result from the cross-validation criterion. Therefore, our second criterion was a minimum increase in R^2 of 0.01 of each split. The smallest size obtained using the two criteria was used to prune the final tree.

Multiple regression

We also modeled patterns in beta diversity using standard multiple-regression models (ordinary least squares, OLS). However, since regression residuals tended to display strong spatial autocorrelation at small distances according to Moran's I correlogram (Diniz-Filho et al. 2003), we also used a spatially explicit simultaneous autoregressive (SAR) error model. Coefficients of SAR and OLS models were relatively similar, so that no red shifts associated with scaling effects of predictors seemed to be affecting SAR results in this particular case (Diniz-Filho et al. 2003, Hawkins et al. 2007a). In the SAR error model, spatial covariance among cells (C) is defined as

$$C = \sigma^2[(\mathbf{I} - \rho\mathbf{W})^{T}]^{-1}\ [(\mathbf{I} - \rho\mathbf{W})]^{-1}$$

where σ^2 is the variance of the residuals, ρ is the autoregressive parameter, and $\mathbf{I}$ is an $n \times n$ identity matrix. The row-standardized $\mathbf{W}$ matrix contains the spatial relationship among sampling units, with elements given by the inverse of the geographic distances (d_{ij}) among them, expressed as $1/d_{ij}^{\alpha}$, where α was chosen to minimize spatially autocorrelated residuals, measured by Moran's I coefficients calculated for 20 geographical-distance classes (Diniz-Filho et al. 2003). All spatial analyses were performed using Spatial Analysis in Macroecology (SAM) software (Rangel et al. 2006), ver. 3.0, freely available at <www.ecoevol.ufg.br/sam>.

Results

The beta diversities of birds and mammals were moderately correlated ($r = 0.54$, Supplementary material, Table S1). The beta diversity of birds was slightly higher (mean = 0.0497) than that of mammals (mean = 0.0393). This is partly due to the greater dispersion of the values for birds (min = 0, max = 0.422, SD = 0.0514) than for mammals (min = 0, max = 0.247, SD = 0.0303) (Supplementary material, Fig. S1).

Beta diversity (β_{sim}) of birds was highest in the Andes, particularly in cells located on slopes (Fig. 1a). However,

low beta diversity predominated in the high plains of southwestern Bolivia (Andean Altiplano) (Fig. 1a). A second region of high beta diversity included the mountainous parts of Central America and Mexico, particularly along the three Sierra Madre mountain ranges (South, Oriental and Occidental). Nevertheless, beta diversity was low in the plateau between the Sierra Madre Oriental and Sierra Madre Occidental. In the United States and Canada, beta diversity tended to be higher in the mountainous west than in the flatter regions of the east. Also, beta diversity was relatively high along the arctic coast of Canada and Alaska. Two regions in South America, not associated with mountains, showed intermediate beta diversity: the narrow strip along the main course of the Amazon River, and the contact region between the Amazon Forest and the Cerrado of Central Brazil. Moderate beta diversity was observed in the coastal Atlantic Forest of Brazil (Fig. 1a).

Patterns of beta diversity for mammals were less distinct than those for birds (Fig. 1b). Beta diversity of mammals was generally high in the Andes, although not very different from surrounding areas in its southern portion. The high beta diversity of birds observed in Central America and Mexico was similarly evident in the map for mammals. However, in contrast to birds, areas of high beta diversity for mammals in western North America extended over part of the Interior Plains. Also, beta diversity of mammals differed from that observed for birds in not showing clear intermediate beta diversity in the Atlantic Forest, in areas along the Amazon River, and in the contact zone of the Amazon Forest and the Brazilian Cerrado.

The cross-validation criterion used to prune trees resulted in large trees, with terminal nodes explaining $<1\%$ of the total variation. We therefore opted to prune trees to the size at which the nodes explained $>1\%$ of the total variation (Fig. 2). This criterion resulted in trees with 8 leaves for both birds and mammals. Only 3 and 5 of the 10 predictor variables were actually used in tree construction using bird and mammal data, respectively. We admit that, because of autocorrelation in model residuals (see below) these results may be somewhat liberal (but see comparison with SAR results, below).

The main factor explaining variation in β_{sim} of birds was difference in altitude (Fig. 3), and in the first node of the tree this predictor explained 52% of the total variation (Fig. 2a). Focal cells differing >618.5 m in altitude from their adjacent cells showed the highest beta diversity (Fig. 2a). For this high beta-diversity group, cells with differences in AET larger than 15.85 cm yr^{-1} usually showed the highest beta diversity among all 4220 cells evaluated. In contrast, cells differing <618.5 m in altitude from their neighbors showed low or intermediate values of beta diversity. For this last group, differences in altitude, again, best explained variation in beta diversity, with high values of beta diversity observed in cells differing by >275.9 m. Similarly to that observed on the right side of the first node of the tree, cells on the left side with large differences in AET showed higher beta diversity than did those with low differences. Differences in PET were also positively related to beta diversity. Except for the first node, each remaining node explained $<6\%$ of the total variation. The tree containing the eight leaves explained 70% of the total variation in beta diversity.

Similar to the tree obtained for birds, the best predictor of beta diversity of mammals was difference in altitude (Fig. 3). However, the tree for mammals differed from the tree for birds in two main respects. First, the variation explained by altitude differences in the first node was much lower in the mammal tree (21%) (Fig. 2b). Second, the effect of differences in altitude was dependent on other variables. For instance, cells differing >476.5 m showed high beta diversity only when differences in PET were larger than 5.6 cm yr^{-1}. On the left side of the first node, high beta diversity was positively associated with differences in AET. This node explained 10% of the total variation. The remaining nodes explained $<3.5\%$ of the total variation. Except for differences in altitude, in which the relationship with beta diversity was dependent on other variables, all remaining variables used in the tree construction were positively associated with beta diversity. The Jaccard distance of Realms (realms.jac) was the only biotic predictor variable selected in the tree for mammals. The 32 cells with realms.jac larger than 0.028 showed, on average, the highest beta diversity over all the cells studied. The total variation accounted for by the tree with 8 leaves was 42.5%.

In general, spatial modeling supported the above conclusions. There was significant spatial autocorrelation in OLS residuals of β_{sim} against the predictors, mainly for mammals (Moran's I in the first class equal to 0.164 for birds and 0.386 for mammals), so that SAR models were also used. The OLS models accounted for 68 and 35% of the variation in spatial beta-diversity patterns of birds and mammals, whereas the full SAR model increased these values to 86 and 64%, respectively (Table 1). The importance rank of the coefficients of each predictor, expressed by t-values, was similar for the two types of models (especially for birds, considering the low levels of residual autocorrelation in OLS).

For birds, the SAR model produced results analogous to those obtained in the regression tree, in which difference in altitude and AET were associated positively with beta diversity. For mammals, the highest partial coefficients in the OLS model were differences in humidity, AET, realms.jac and ecoregions.jac; whereas in SAR the same predictors were important in general (Table 1). However, these coefficients in SAR were more similar, suggesting greater uncertainty in establishing the best predictors for mammals, and that patterns of beta diversity were less clear for this group. The results for mammals were in partial agreement with the tree obtained for mammals, in which most of the best predictors were the same. However, they differed in the order of importance. For instance, the tree regression indicated that difference in altitude was the best predictor, and that difference in humidity explained a very small fraction of the total variation. In the OLS and SAR models, the importances of these two predictors were reversed.

Discussion

Our conclusions from the tree regression results are not based on probability values, so that residual spatial autocorrelation is not expected to shift our interpretation (see also Hawkins et al. 2007a). This is supported because the results from explicit spatial regression modeling using

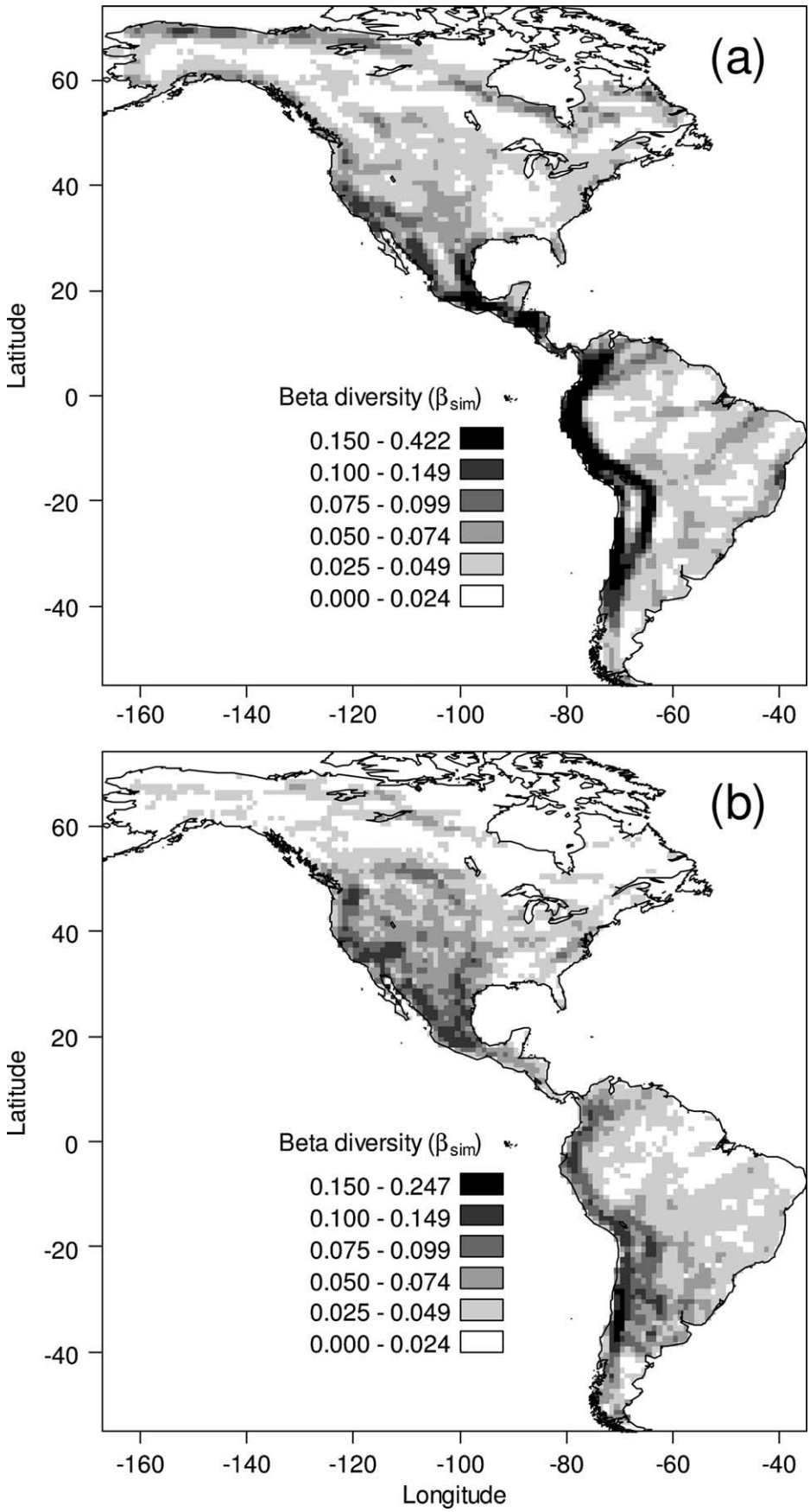

Figure 1. Beta diversity of New World birds (a) and mammals (b) calculated using the average of the β-sim index among a focal cell and all its adjacent cells. Each cell covers 1 degree of latitude and longitude.

SAR and OLS were qualitatively similar to those from tree regression. For birds, the rank of predictors between SAR and tree regression was similar, but not for mammals, although the differences in ranks of main predictors can be easily understood by model instability generated by multicollinearity. Following Diniz-Filho et al. (2008), we also made exhaustive search of all possible OLS models (i.e. with different combinations of predictors) based on Akaike information criterion (not shown, to conserve space). Indeed, the predictors previously discussed were exactly those that had the highest importance values in multimodel inference (i.e. weighted average of several models). Thus, the overall correspondence between main predictors in SAR, OLS and the regression tree reinforces this issue and indicates the robustness of the conclusions reached.

Beta-diversity values of birds and mammals were highest in mountainous areas, where large differences in altitude and temperature occur over short distances. Concordant with our results obtained at the continental scale, Herzog et al. (2005) studied elevational gradients of Andean birds and found high turnover due to differentiation of lowland and upland faunas. It is unlikely, however, that differences in altitude or the correlated difference in temperature themselves directly affect beta diversity. Instead, the two variables are surrogates

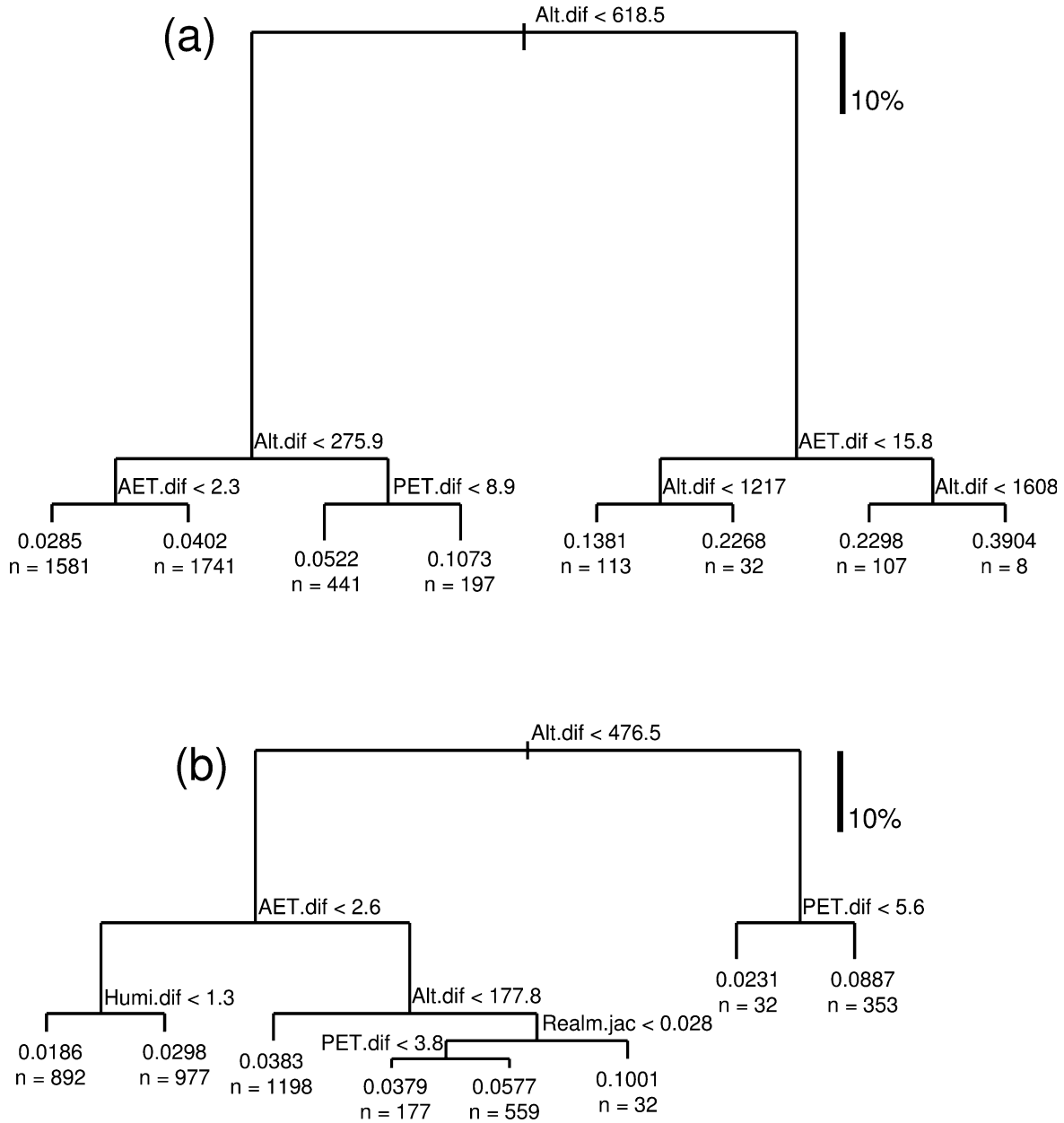

Figure 2. Regression tree analysis of beta diversity of (a) birds and (b) mammals. Vertical lines are proportional to the reduction in residual error. The suffix ".dif" indicates that the predictor variable consists of the mean difference between the focal cell and all the adjacent cells. The suffix ".jac" indicates that the predictor variable was obtained by calculating the mean Jaccard distance among the focal cell and all adjacent cells. Numbers at the bottom of the tree indicate the average beta diversity and the number of cells classified at each leaf. Alt = altitude. AET = actual evapo-transpiration. PET = potential evapo-transpiration. Humi = humidity. Realm = realms. See text for further information on how predictors were obtained.

for habitat differentiation (see Dufour et al. 2007 for a small-scale example). In fact, in the study of Mourelle and Ezcurra (1997), high beta diversity of cacti was observed in topographically heterogeneous areas, where a number of biogeographic provinces meet.

High beta diversity among regions implies that historical processes of isolation are creating divergence in species composition among these regions. In this context, variation among cells can be directly interpreted as resulting from differentiation of the species pool, in which the underlying mechanistic and populational basis is geographical range differentiation. Among the predictors used, difference in altitude is indeed the most appropriate surrogate for this divergence in species composition.

However, it is difficult to decouple the historical and ecological processes that may affect the divergence of species pools. For instance, Hawkins and Diniz-Filho (2006) recently demonstrated the importance of altitude and temperature, and their interactions, in explaining geographical variation in average range sizes throughout the New World (see also Ruggiero and Hawkins 2008). Although this study revealed that average range sizes are driven by ecological processes, no explicit tests of historical components that might be associated with these geographic variations were applied. Additional approaches could be used to directly model evolutionary processes at species level (Weir 2006, Hawkins et al. 2007b), and could be adapted to attempt to decouple these components in the future.

The map of beta diversity for birds (but not mammals) showed relatively high values along the Amazon River and in the contact region of the Amazon forest and Cerrado savanna (see also McKnight et al. 2007). In fact, previous studies have shown that the flooding regime of the large rivers in the Amazon basin results in distinct vegetation types (várzea, igapó and upland forests) in adjacent areas (Wittmann et al. 2006). High beta diversity of birds along the main Amazon rivers may thus be a result of habitat specialization or the presence of range-restricted species (Kark et al. 2007). On the other hand, large rivers (and past marine incursions into the eastern Amazon basin) may act as barriers to gene flow for birds and thus favor allopatric speciation (Aleixo 2004). Despite these two potential mechanisms to explain high beta diversity of birds along the Amazon River, the dissimilarity in biotic units between the focal cell and its adjacent cells was unimportant for the explanation of variation in beta diversity of birds. This is partially at odds with the finding of van Rensburg et al. (2004) that high beta diversity of birds in South Africa coincided with transition zones between biomes (see also Williams 1996). For mammals, results from the tree regression indicated that biotic units were unimportant, although the OLS and SAR models indicated the opposite. Results from van Rensburg et al. (2004) and McKnight et al. (2007) showed that regions of highest beta diversity for New-World mammals, birds and amphibians were correlated with both mean altitude and the number of biome boundaries. However, van Rensburg et al. (2004) also showed that transition zones were associated with high climatic heterogeneity, making it difficult to infer a

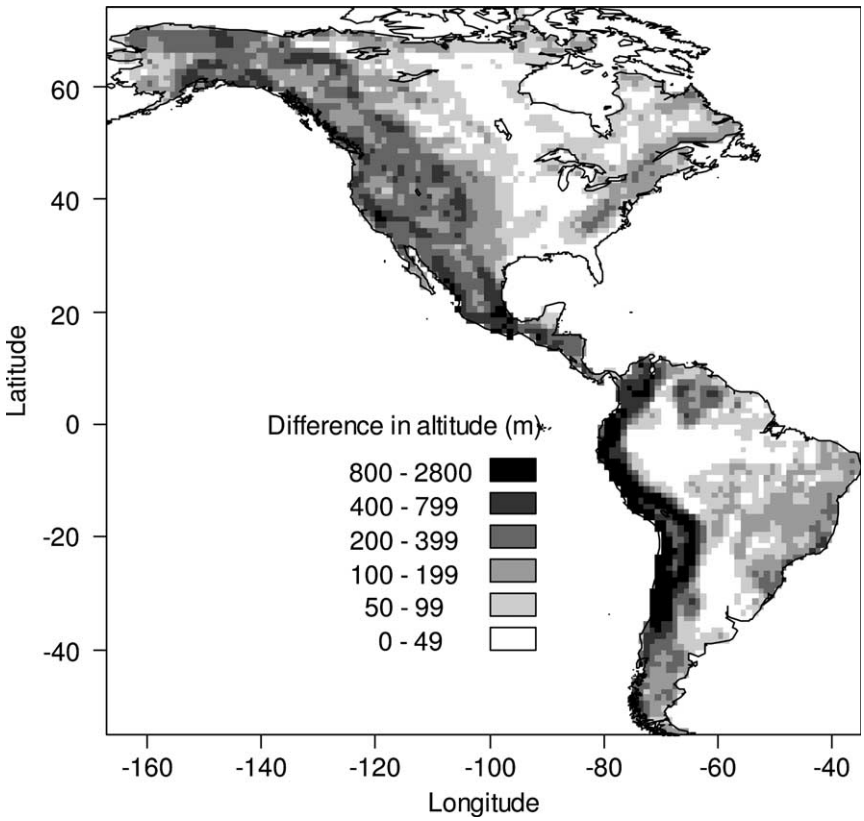

Figure 3. Average differences in altitude among a focal cell and all its adjacent cells, the best predictor of beta diversity of New World birds and mammals. Each cell covers 1 degree of latitude and longitude.

Table 1. Results of ordinary least squares (OLS) and simultaneous autoregression (SAR) models for beta-diversity in New World birds and mammals, including the standardized coefficient (b) and the associated t-value for each predictor. See Methods for definition of variables.

Predictor	Birds				Mammals			
	OLS		SAR		OLS		SAR	
	b	t	b	t	b	t	b	t
AET.dif	0.23	13.26**	0.15	10.28**	0.13	5.09**	0.08	4.18**
Alt.dif	0.63	38.46**	0.59	36.81**	0.08	3.59**	−0.06	3.35**
PET.dif	0.03	1.62	−0.06	−3.76**	0.15	5.80**	0.06	3.35**
NPP.dif	0.02	1.56	−0.03	−4.93**	0.01	0.71	−0.02	1.81
Preci.dif	0.06	4.71**	0.05	3.80**	−0.04	2.36*	0.01	0.86
Humi.dif	−0.04	−3.30	−0.02	−1.35	0.28	14.74**	0.09	4.97**
Biomes.jac	0.03	2.37*	0.02	1.99*	0.04	2.56*	0.01	0.53
Realms.jac	0.03	3.51	0.01	1.46	0.13	10.47**	0.03	2.47*
Ecoregions.jac	0.02	1.64	0.16	1.31	0.17	9.62**	0.08	5.28**
Polygons.jac	−0.01	−0.84	0.02	1.39	−0.08	4.62**	0.01	0.05

*$p < 0.05$; **$p < 0.01$

cause-and-effect relationship between beta diversity and the heterogeneity of biotic units.

Our fitted models explained much more of the variation in beta diversity of birds than of mammals. Also, the beta-diversity map of mammals was less distinct, not strongly associated with obvious environmental characteristics (e.g. topography in the case of birds). Two points should be considered in interpreting the differences in beta-diversity patterns of the two groups. First, most of the total variation in beta diversity of birds is related to a few cells that were very different in altitude and associated with very high beta diversity (right side of the first node of the regression tree [Fig. 2]) (Supplementary material, Fig. S1). Accordingly, decreasing the spatial extent of the study (e.g. excluding the Andes) may produce models explaining proportionally less variation. Apparently, the distinctiveness of mammal faunas in cells that differ greatly in altitude from their neighborhood is not so pronounced as that for birds. The second possibility to explain the difference in fitness of the models for birds and mammals stems from the finding of Rodríguez and Arita (2004), that different groups of mammals show different broad-scale beta-diversity patterns in North America. For instance, they showed that beta diversity of bats is not related to latitude, although a negative latitudinal gradient in beta diversity for non-volant mammals was present. In this context, the poor fit of our models to the mammal data may be a consequence of the heterogeneity in responses of its constituent groups.

Habitat heterogeneity, measured as the variability in elevation within a region, has also been mentioned as a good predictor of mammal species richness in high-energy regions (PET >1000 mm yr^{-1}) (Kerr and Packer 1997). In this case, high values of species richness in regions with PET >1000 mm yr^{-1} are likely the summed result of alpha and beta diversities at smaller scales: abundant energy is a predictor of species richness ''within'' habitats (alpha) (Hawkins et al. 2003), and habitat heterogeneity is a predictor of beta diversity among localities within a region (Veech and Crist 2007).

Patterns of species richness in New-World and South-American birds have been analyzed in many recent studies (Rahbek and Graves 2001, Hawkins et al. 2003, 2007a). Especially for South America, the effects of altitude and its interaction with other climate data, especially an interaction with temperature (or latitude), are usually important predictors in all the models (see also Rahbek and Graves 2001, Hawkins and Diniz-Filho 2006). Additionally, an important portion of variance in richness can be explained by combined effects of energy and water availability (AET; Hawkins et al. 2003, 2007b). However, in the Andean region, the unexplained residual structure (i.e. higher species richness than predicted by models of climate and altitude) is usually attributed to greater environmental instability and heterogeneity at lower scales, which create barriers that, in turn, accelerate diversification events (Weir 2006). Since we are not modeling the number of species per se, but instead we are assessing directly the distinctiveness in species composition of each cell, the best predictors of beta-diversity, obtained both by tree regression and SAR model, supported this explanation for birds and partially for mammals. This rationale is concordant with the findings of Kerr and Packer (1997) that habitat heterogeneity at smaller scales is a good predictor of mammal species richness in high-energy regions, and of Veech and Crist (2007) that both habitat (elevational range) and climate (coefficient of variation for PET) heterogeneity are related to beta diversity of North American birds at multiple spatial scales.

Finally, as in any other broad-scale diversity analysis, the patterns found may be partially affected by decisions regarding grain size (Lennon et al. 2001). We used here a standard grain size of 1° cell, which has been used in many recent New World and global analyses (Orme et al. 2005, Hawkins et al. 2007a, b, Rangel et al. 2007). However, Hurlbert and Jetz (2007) pointed out that coarser grain sizes might be more appropriate. Although we are aware of these scaling problems, there are two main issues that are important to consider and that, in our point of view, minimize this problem. We are analyzing the data in a spatially explicit context, so that pseudoreplication associated with the finer grain size of 1° cell was taken into account in SAR modeling. Second, we tested different ways to calculate beta diversity, by increasing the neighbor size (i.e. calculating beta diversity for the 24 and 48 cells in second- and third-order adjacencies) and this did not qualitatively affect the patterns described here.

Our analysis of continental patterns of beta diversity in mammals and birds showed that heterogeneity in habitat

and climate conditions explain geographical variation in composition among regions, independently of the amount of richness. Although further studies are necessary to attempt to decouple the effects of current adaptation of species to particular environmental conditions by range shifts or species' divergence by vicariance, both creating geographical structures in beta diversity, our analysis showed how variation in species composition among regions can be directly interpreted as resulting from differentiation of the species pool.

Acknowledgements – A. S. Melo received research grants from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPQ no. 476256/2004-6, 476304/2007-5) and the International Foundation for Science (IFS no. A/4107-1). Work by J. A. F. Diniz-Filho is supported by CNPq grants 301259/2005-4 and 470918/2006-3. T. F. V. B. Rangel receives a CAPES/Fulbright Doctoral Fellowship. Janet Reid reviewed the English. Thomas Crist and four anonymous referees provided extensive constructive suggestions for the manuscript. We extend our appreciation to all the people who gathered and organized the data used in this study.

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