

Species Richness and Evolutionary Niche Dynamics: A Spatial Pattern–Oriented Simulation Experiment

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Submitted November 27, 2006; Accepted May 14, 2007;
Electronically published August 9, 2007

Online enhancements: appendixes.

ABSTRACT: Evolutionary processes underlying spatial patterns in species richness remain largely unexplored, and correlative studies lack the theoretical basis to explain these patterns in evolutionary terms. In this study, we develop a spatially explicit simulation model to evaluate, under a pattern-oriented modeling approach, whether evolutionary niche dynamics (the balance between niche conservatism and niche evolution processes) can provide a parsimonious explanation for patterns in species richness. We model the size, shape, and location of species' geographical ranges in a multivariate heterogeneous environmental landscape by simulating an evolutionary process in which environmental fluctuations create geographic range fragmentation, which, in turn, regulates speciation and extinction. We applied the model to the South American domain, adjusting parameters to maximize the correspondence between observed and predicted patterns in richness of about 3,000 bird species. Predicted spatial patterns, which closely resemble observed ones ($r^2 = 0.795$), proved sensitive to niche dynamics processes. Our simulations allow evaluation of the roles of both evolutionary and ecological processes in explaining spatial patterns in species richness, revealing the enormous potential of the link between ecology and historical biogeography under integrated theoretical and methodological frameworks.

Keywords: niche conservatism, birds, South America, simulation model, latitudinal gradient, diversity gradients.

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Am. Nat. 2007. Vol. 170, pp. 602–616. © 2007 by The University of Chicago. 0003-0147/2007/17004-4224\$15.00. All rights reserved.
DOI: 10.1086/521315

As early as the eighteenth and nineteenth centuries, naturalists described and documented what we today call geographical gradients in taxon diversity (species richness), especially the general global pattern of increase in species richness toward warm and wet tropical regions (Whittaker et al. 2001; Hawkins et al. 2003b; Willig et al. 2003; Hillebrand 2004). Initial hypotheses explaining this pattern were deduced solely by observing and describing nature and were based on nothing more rigorous than intuitive correspondence between climatic and biological patterns (Hawkins 2001). Surprisingly, even after 200 years of research in biogeography and ecology, the most common framework used in such investigations still relies on statistical measurements of the concordance between the spatial patterns in species richness and multiple environmental factors. The generally strong relationship between species richness and some of these environmental factors (e.g., Hawkins et al. 2003a) has led many researchers to conclude that environment (e.g., climate) is the main driver of species richness, based on a purely correlative view (see Hawkins et al. 2003b). Until recently, the processes underlying these correlations were usually defined by verbal arguments without formal modeling or even clear epistemological structures (but see Currie et al. 2004; Scheiner and Willig 2005). However, in the past decade, more complex models were developed to evaluate environmental or climate-based hypotheses, based on the effect of environmental variables on organismal metabolism and physiology or on population dynamics (see Allen et al. 2002; Field et al. 2005; O'Brien 2006). Despite these advances, the evolutionary components underlying these correlations between climate and species richness remain poorly understood (Ricklefs 2006).

In contrast with climate-based hypotheses, evolutionary hypotheses have developed since the early 1960s as almost independent sets of explanations (Ricklefs 2004, 2006; Mittelbach et al. 2007). In general, evolutionary hypotheses invoke a geographical (i.e., latitudinal) bias in net diversification rates (for recent evaluations, see Cardillo et al.

2005; Weir and Schluter 2007) driven by area availability (Rosenzweig 1995) or climatic factors (Wright 1983; Rohde 1992, 1999; Wright et al. 1993). A geographical bias in net diversification rates has been suggested to be caused by a spatially patterned buffer against extinction (Hawkins et al. 2005, 2006) or by an acceleration of tropical speciation rates due to metabolic activation (Rohde 1992; Bromham and Cardillo 2003; Allen et al. 2006). The most common approach to studying these evolutionary hypotheses attempts to decouple the effects of “ecological” (contemporary) and “evolutionary” (historical) components of the spatial patterns in species richness (e.g., Hawkins et al. 2003*b*; Diniz-Filho et al. 2004; Bjorholm et al. 2006), although usually one or the other is simply ignored or credited with unexplained variation.

However, as highlighted by Wiens and Donoghue (2004) and Hawkins et al. (2005), historical biogeography and ecology have much to offer each other, and perhaps a better approach would be to join the two perspectives into a unified theoretical and analytical framework capable of resolving the tangled and/or interactive effects of both ecological and evolutionary processes affecting species richness (Ricklefs 2006). Furthermore, Currie et al. (2004), who recently reviewed those hypotheses that invoke climatic factors to explain spatial patterns in species richness under a hypothetical-deductive, Popperian approach, concluded that these hypotheses are still very difficult to evaluate and that the biological underlying mechanisms that link climate to species richness remain to be discovered.

Phylogenetic niche conservatism (Harvey and Pagel 1991; Peterson et al. 1999; Ackerly 2003; Holt 2003) refers to an evolutionary pattern in which descendant species tend to share, by common descent, a substantial proportion of the biological and physiological characteristics that determine their fundamental ecological niches (Hutchinson 1957). Thus, the adaptations of a common ancestor to a particular set of environmental conditions (i.e., the ecological zone of origin; Holt and Gaines 1992; Holt 1996; Wiens 2004) tend to be conserved in descendant species, with little adaptive biological modification (e.g., Ricklefs and Latham 1992; Ricklefs 2006). Whether a particular pattern of niche conservatism is the result of constraints on adaptive evolution (e.g., absence of appropriate genetic variation) or simply a consequence of diversification in widespread, uniform environments probably depends on the case in question. Niche conservatism is a key component of a recent verbal model of the expected effects of environmental fluctuation on the evolution of a species' ecological niche and the consequences for biogeographical (Ackerly 2003; Wiens 2004; Wiens and Donoghue 2004; Wiens and Graham 2005) and community assembly patterns (Webb et al. 2002; Ackerly 2003).

In contrast, niche evolution refers to evolutionary change,

during or immediately following speciation events, in the traits that define the niche, allowing descendant species to adapt rapidly to new environmental conditions (Wiens and Donoghue 2004). Thus, it has been hypothesized that if niche conservatism prevails over niche evolution in regions of highly heterogeneous and/or asynchronously fluctuating environments, diversification might occur predominantly by a process of range fragmentation, caused by the inability of species to adapt to changing environmental conditions in portions of the ancestral range (Wiens 2004; Wiens and Donoghue 2004). In this scenario, once environmental fluctuation has fragmented a species' geographical range into isolated populations (Dynesius and Jansson 2000; Jackson and Overpeck 2000; Jansson and Dynesius 2002; Ackerly 2003; Wiens 2004), geographic (and eventually reproductive) isolation of those isolated populations would lead to allopatric speciation (see also Kirkpatrick and Barton 1997; Holt 2003) and possibly adaptive radiation (Gavrilets and Vose 2005).

The balance between niche conservatism and niche evolution may also have played an important role in determining contemporary geographical gradients in species richness (Wiens and Donoghue 2004; Wiens and Graham 2005; Ricklefs 2006). According to this hypothesis, most clades originated under a tropical climatic regime, which had, for most of Earth's history, and still has, greater geographical extent and environmental stability than extratropical climates (Wallace 1878; Stephens and Wiens 2003; Wiens and Donoghue 2004; Hawkins et al. 2005; Jablonski et al. 2006). If descendant lineages tend to conserve ancestral niche characteristics (e.g., Ricklefs and Latham 1992), then clades may have been slow to spread toward extratropical regions or are now extinct in those regions that are not tropical anymore (e.g., Hawkins et al. 2005, 2006). Such a process would tend to generate a higher richness in the ecological zone of origin (tropical regions) because of a higher net diversification rate, whereas species in more recently derived clades could potentially become adapted to temperate conditions, breaking away from phylogenetic constraints on niche characteristics (the “out of tropics” model; e.g., Jablonski et al. 2006). Thus, the tropics would be both the “cradle” and the “museum” of species diversity (Jablonski et al. 2006).

To evaluate whether an appropriate balance between niche conservatism and niche evolution could potentially explain spatial patterns in species richness on a geographic scale, we developed a spatially explicit simulation model of niche evolution. The simulation approach is especially suitable for this study because it allows us to unravel and describe complex patterns (Winsberg 1999; Peck 2004; Grimm et al. 2005) that are simultaneously driven by multiple biological processes (Peck 2004) and independent agents (e.g., species and their geographical ranges; Grimm

et al. 2005), in both spatial and temporal dimensions (Naylor et al. 1966). Furthermore, we used the simulation model as an ecologically controlled quasi experiment (Peck 2004) in which some factors may be held constant in order to study the isolated and/or interactive effects of other ecological and evolutionary processes on the emergent patterns (Winsberg 2003; Peck 2004). Our simulation model was also used as a predictive model, which offers a special advantage over correlative models because it provides predictions in units of species richness (number of species co-occurring at the same place and time), allowing much more robust statistical inferences (Colwell et al. 2004; Rahbek et al. 2007). Only a few recent studies have used simulations to test alternative scenarios to distinguish among competing hypotheses (in contrast to the traditional correlative approach; e.g., Hawkins et al. 2003b), most of them in the context of geometric constraint models (e.g., Colwell and Lees 2000; Bokma et al. 2001; Jetz and Rahbek 2001; Davies et al. 2005; Rangel and Diniz-Filho 2005a, 2005b; Rahbek et al. 2007).

We used empirical spatial patterns in species richness and range size frequency distribution of South American bird species to guide our model parameterization and analyses (a pattern-oriented modeling approach; sensu Grimm et al. 2005). Our primary goal was to investigate the influence of niche conservatism and niche evolution (as outlined in Wiens 2004; Wiens and Donoghue 2004), acting over broadscale heterogeneous landscapes, on those predicted patterns that most closely resemble observed patterns. We found that in models that account for a substantial portion of the variation in both spatial patterns of richness and range size frequency distribution in South American birds, model fit is quite sensitive to the level of niche conservatism. We conclude that niche dynamics models can provide a plausible explanation for broadscale biogeographical patterns in species richness.

Methods

Model Overview

Our model simulates the dynamics of species' geographical range size, shape, and placement over a multivariate heterogeneous environmental landscape by stochastically defining each species' fundamental niche as an inherited set of environmental tolerances, evolving in the context of a dynamically fluctuating environment. The environmental dynamics follow a regular cycle through time, forcing the fragmentation of geographical ranges, driving both speciation and extinction (Wiens 2004). The model can be used to assess which combinations of model parameters generate realistic patterns of species richness, range size frequency distribution, and evolutionary components of

diversification (Wiens and Donoghue 2004; Wiens and Graham 2005); it was applied to allow better understanding of the evolutionary drivers of patterns of contemporary bird species richness in South America.

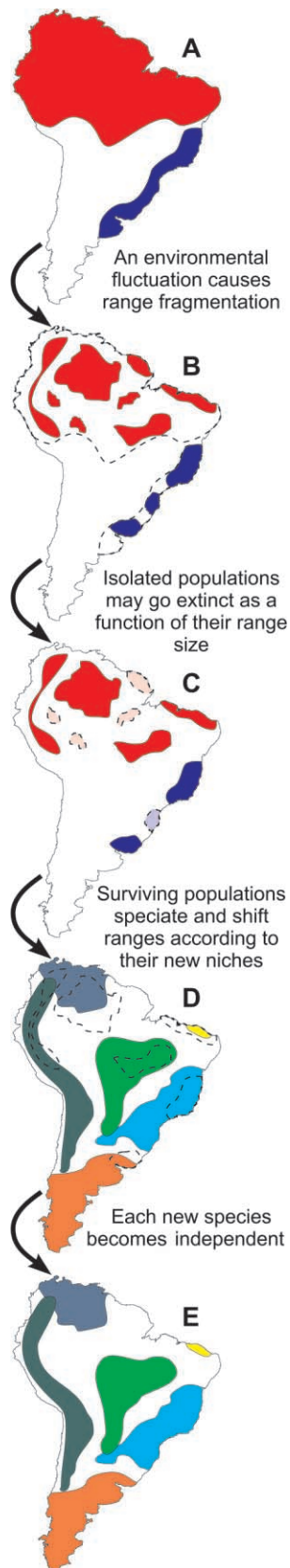
Conceptually and computationally, our model consists of two linked components: an n -dimensional niche space and a two-dimensional geographical map space (a discrete, virtual domain modeled as a lattice). Each cell on a gridded map is characterized by its geographical coordinates and by the local values of the same n environmental parameters that define the niche space (a representation pioneered by Pulliam [2000]). We used the South American continent, divided into $1^\circ \times 1^\circ$ cells ($m = 1,565$), as the geographical domain for this study. By mapping the values of n observed environmental variables ($e = 1, 2, \dots, n$; see next section) in each grid cell, environmental spatial patterns were established. We studied the individual and combined influence of six observed variables that describe the heterogeneous environmental conditions across South America: (1) actual evapotranspiration, (2) potential evapotranspiration, (3) minimum annual humidity, (4) maximum annual humidity, (5) minimum annual temperature, and (6) maximum annual temperature (New et al. 1999; Kucharik et al. 2000; Willmott and Kenji 2001). Each of these six factors represented a niche axis in the simulation model, each exerting equal control over simulated species.

The basic unit of our model is the species, evolving through time and characterized by three state variables: species' niche center, niche breadth, and range size (table A1 in the online edition of the *American Naturalist*). Thus, after Hutchinson (1957), the niche is considered a property of each species, defined by its adaptive tolerances along each niche axis, not as a preexisting unit of the environment. Time is measured in discrete steps on an evolutionary (rather than demographic or ecological) scale.

Model Dynamics

The simulation begins by randomly placing the first species into a single, randomly selected cell (model parameters G_{lat} and G_{long} are its coordinates). The values of the n environmental variables in the initial cell define the optimal environmental conditions (niche center) for the initial species. Next, symmetrical deviations (niche breadth) around the species' optimal environmental value, for each niche axis, are stochastically defined by model parameter σ . The species is then allowed to expand its range cohesively on the map, immediately occupying any other spatially contiguous cells for which all environmental conditions lie within the corresponding upper and lower tolerance limits for this species in niche space.

At each time step, the values assigned to the environmental variables on the map increase or decrease according



to a sine wave, which can be defined by two parameters: amplitude (A) and frequency (f). The first controls the magnitude of change at the point of maximum increase or decrease of the environmental fluctuation cycle (e.g., glacial maxima/minima) and is defined as percentage of the magnitude of each environmental variable in each map cell. At each time step, all environmental variables change synchronously by the same proportion in every map cell, driven by a single master sine wave. The second parameter, f , controls the number of cycles completed during each model run.

In the model, environmental fluctuations may trigger biogeographical events, such as changes in location, size, and shape of each species' geographical range (fig. 1). In addition, environmental fluctuations may cause fragmentation of a species' geographical range. The range fragments then represent isolated populations (fig. 1). These isolated populations can become extinct as an inverse function of their geographical range size, and the decrease in the probability of extinction, P_x , was modeled by the function $P_x = -\ln(r/m)/(1/\alpha)^2$, where α is a parameter that varies between 1 (high extinction probability) and a very small number (~ 0 ; low extinction probability), r is the range size of the isolated populations, and the parameter m is the smallest range size for which the probability of extinction is 0 (i.e., for $r \geq m$, $P_x < 0$, and is thus set to 0; fig. A1 in the online edition of the *American Naturalist*). This function also controls the possible extinction of species with unfragmented ranges as a function of range size.

After fragmentation, any surviving populations become new and independent species. When a newly isolated population (a range fragment) becomes a new species, its niche center is adaptively shifted to a point in niche space somewhere between the niche center of its parent species (niche conservatism) and the mean local environmental conditions of its new geographical range (niche evolution). The magnitude of this shift in the niche center is controlled by the parameter Δ . At the same time, niche breadth (tolerance limits) along each niche axis for the new species is

Figure 1: A, Geographical ranges of two hypothetical, ancestral species are subjected to environmental fluctuation (*red and blue areas*). B, After environmental fluctuation, species' geographical ranges (*white areas, dashed outlines*) may become fragmented into smaller, isolated populations (*red and blue areas, solid outlines*), with variable range size. C, Each fragment may become extinct as a function of its geographical range size (*light red and blue areas, dashed outlines*) or may survive (*dark red and blue areas, solid outlines*). D, Each surviving population speciates and expands its geographical range (*white areas, dashed outlines*) to colonize areas within its new ecological niche (*colored areas, solid lines*; see text for details on how the niches of new species are defined). E, New species become independent (*colored areas*).

also inherited from the parent species, with a degree of conservatism/evolution set by model parameter ω . Thus, the larger the parameters Δ and ω are, the more a descendant species' niche center and breadth may differentiate from those of the ancestor species' niche (niche evolution). Because speciation processes occur in an allopatric mode over spatially autocorrelated environments and, primarily, because of the high carryover of niche center and breadth from ancestral to descendant species, patterns in species richness will evolve under a process of high "heritability" in niche space, consequently conserving range size and geographical location (see Webb and Gaston 2003, 2005; Hunt et al. 2005).

Once a descendant species' niche characteristics are defined, its geographical range immediately spreads cohesively on the map, occupying all contiguous, suitable cells. All new species resulting from this speciation process are then subjected to the same simulation rules in the next time step. One single simulation is finished when a predefined number of time steps (i.e., environmental fluctuations) has been reached. The entire simulation is repeated (the procedure is replicated under the same conditions), and the results are averaged among replicates. For a detailed description of the model, algorithms, and equations, following a standard protocol for describing agent-based models (Grimm et al. 2006), see appendix A in the online edition of the *American Naturalist*.

Simulations

To explore the parameter space and evaluate the model's predictive power for observed patterns, we performed a total of approximately 15,000 sets of replicated simulations, each set with different parameter combinations, using a grid computing platform (see app. A). Each simulation was replicated 100 times (the entire process thus required 1.5 million simulations), although previous analysis showed that results for any particular parameter combination become stable at about 45 replicates. Each replicate was run for 40 time steps. Preliminary analyses showed that model predictions, as measured by proportional richness among map cells, are independent of the number of time steps and independent of the frequency (f) and amplitude (A) of environmental fluctuations because those parameters affect only the pace of the diversification process and the expected absolute size of species pool at the end of the simulation. Thus, we set the model to perform two complete sine waves (f), with the amplitude of increase and decrease of environmental variables (A) fixed at 10% (fig. B1 in the online edition of the *American Naturalist*). The frequency and amplitude were fixed at these levels in order to generate a simulated species

pool of around 3,100 species, approximately matching the number of observed species (3,088).

We performed simulations for which the niche space was defined by each environmental variable alone and by multiple combinations of the six environmental variables in order to find the combination that maximizes the fit between observed and predicted patterns in species richness. We let the parameters G_{lat} and G_{long} , which define the geographical position of the range of the initial species, vary randomly among replicates. For the parameter σ , which regulates the breadth of initial species' niche, we used 10 different values ($0.25 < \sigma < 1.5$). The parameters Δ and ω , which jointly regulate the niche conservatism/evolution processes, each assumed 10 different values ($0 < \Delta < 1$; $0 < \omega < 1.5$). The parameter α , which regulates the strength of extinction probability as function of range size, also assumed 10 different combinations ($0.05 < \alpha < 0.5$). The scope of exploration of parameter space and the best combinations of parameter values are shown in table 1.

Data Analysis

We used a pattern-oriented modeling approach (Grimm et al. 1996, 2005) to find the combination of parameters that maximizes the similarity between the predicted and observed spatial patterns in species richness and range size frequency distribution for a total of 3,088 South American birds (fig. 2A). The digitized bird database (Ridgely et al. 2005) was processed using ESRI ArcView 3.1 scripts to record each species' presence, as defined by its breeding range, in the $1^\circ \times 1^\circ$ grid cells ($m = 1,565$) covering South America. We calculated observed spatial patterns in species richness by summing the number of species presences in each cell and determined range size by summing the number of cells in which each species is present.

Because of the complexity of the model and wide range in parameter variation, we followed a sequential approach in which the most promising scenarios were selected for closer examination, while parameter combinations that produced poor fits were discarded. Initially, we used Pearson's correlation coefficient (r_p) between predicted and observed spatial patterns in species richness to find the parameter combination that maximized model predictive power. However, since broadscale patterns in species richness are usually strongly spatially autocorrelated (Diniz-Filho et al. 2003; Rangel et al. 2006), we performed the significance test of r_p using the number of degrees of freedom estimated by Dutilleul's (1993) method, which accounts for spatial autocorrelation in both variables, and discarded any nonsignificant correlations between predicted and observed patterns.

After first maximizing model fit with respect to spatial patterns in species richness, we used the fit of the observed

Table 1: Parameters of the model with their respective notations, values explored, and best sets

Model parameter	Symbol	Explored	Best set
Geographical position (lat., long.) of the initial species	$G_{\text{lat}}, G_{\text{long}}^a$	Random feasible	$G_{\text{lat}} = 4.5^\circ \text{ S}, G_{\text{long}} = 57.5^\circ \text{ W}$
Initial niche breadth	σ	.25–1.5	.8
Niche center conservatism	Δ	0–1	.2
Niche breadth conservatism	ω	0–1.5	.05
Extinction pressure as a function of species' range size	α	.05–.5	.08
Environmental variables	$e = 1, 2, \dots, n$	AET, PET, min. and max. temperature, min. and max. humidity	Min. and max. temperature, min. and max. humidity

Note: Fit for best set, with standard deviations: $r_p = 0.892 \pm 0.063$, $D = 0.256 \pm 0.174$. Best set is the averaged parameter combination among the 25 best predictions that simultaneously maximize model predictive power of the observed spatial patterns in species richness (r_p , 95% confidence interval [CI] = 0.866–0.918) and range size frequency distribution (Kolmogorov-Smirnov D , 95% CI = 0.184–0.327). AET = actual evapotranspiration; PET = potential evapotranspiration.

^a Parameter does not significantly influence model predictive power.

and predicted range size frequency distributions (RSFDs) as a secondary criterion to further refine model evaluation and selection. In our model, the RSFD is a good criterion for evaluation of model realism because it is interactively driven by virtually all model parameters and processes, such as the spatial pattern in the environmental variables (e), the niche breadth of the initial species (σ), the degree of conservatism of niche breadth along the simulations (ω), and the extinction pressure as function of geographic range size (α). We used the statistic D of the Kolmogorov-Smirnov two-sample nonparametric test to measure the differences between the shapes of the observed and predicted RSFDs. The variable D is the maximum unsigned difference between two relative cumulative frequency distributions (the observed and predicted RSFD, in our study) and is sensitive to differences in location, dispersion, skewness, and kurtosis (Sokal and Rohlf 1995). The value of D ranges from 0 to 1 and is small for two frequency distributions with a close fit.

Next, we performed a more detailed statistical analysis of the regression between observed and predicted spatial patterns in species richness for the 25 best simulations, as judged by higher r_p and lower D . Because our model yields predictions in units of species, we can assess not only the magnitude of fit (r_p) but also the accuracy of the predictions by the regression coefficients. The closer the intercept is to 0 and slope is to 1, the more accurate is the model prediction. Thus, we started by using an ordinary least squares (OLS) regression analysis to find the intercept and slope values and then used Moran's I (calculated for five distance classes, with equal numbers of pairs of grid cells) to assess the magnitude of spatial autocorrelation in the residuals of the OLS regression (see Diniz-Filho et al. 2003). For cases in which the residuals of this regression were spatially autocorrelated (our criterion was Moran's $I_{0-1,000 \text{ km}} > 0.2$ and/

or $I_{1,000-1,600 \text{ km}} > 0.1$), we abandoned the OLS regression and used simultaneous autoregressive models (SARs) to find more accurate intercept and slope values (Cressie 1993). We report the averaged mean and 95% confidence intervals (CIs) for the intercept and slope of the 25 best predictions. All OLS and spatial statistics were carried out using SAM, version 1.1 (Rangel et al. 2006), freely available at <http://www.ecoevol.ufg.br/sam>. Finally, an ANOVA (model II ANOVA; Sokal and Rohlf 1995) was used to evaluate the influence of model parameters (each parameter as a factor) on the correlation coefficient (r_p , after z transformation) calculated between observed and predicted spatial patterns in species richness and on Kolmogorov-Smirnov D calculated between observed and predicted RSFDs.

Results

Bird species richness is strongly spatially patterned over South America, although the patterns are very complex (fig. 2A). Some regions such as the Amazon Basin and the Atlantic Forest are highly species rich; these regions generally lie along a NW-SE axis of South America. Another very species-rich axis lies along the Andean mountains, on the west coast of South America, from the center of Bolivia to northern Venezuela (see also Rahbek and Graves 2001; Hawkins et al. 2006). On the other hand, there are also species-poor regions, such as the Atacama Desert and Brazilian Caatinga, which are approximately aligned in a NE-SW direction. Under medium-scale patterns such as those we used, a clear gradient in species richness over the whole continent is apparent, with richness decreasing toward higher latitudes. The observed range size frequency distribution for birds in South America matches the strongly right-skewed (fig. 3A) pattern commonly observed in nature at this scale (Gaston 2003).

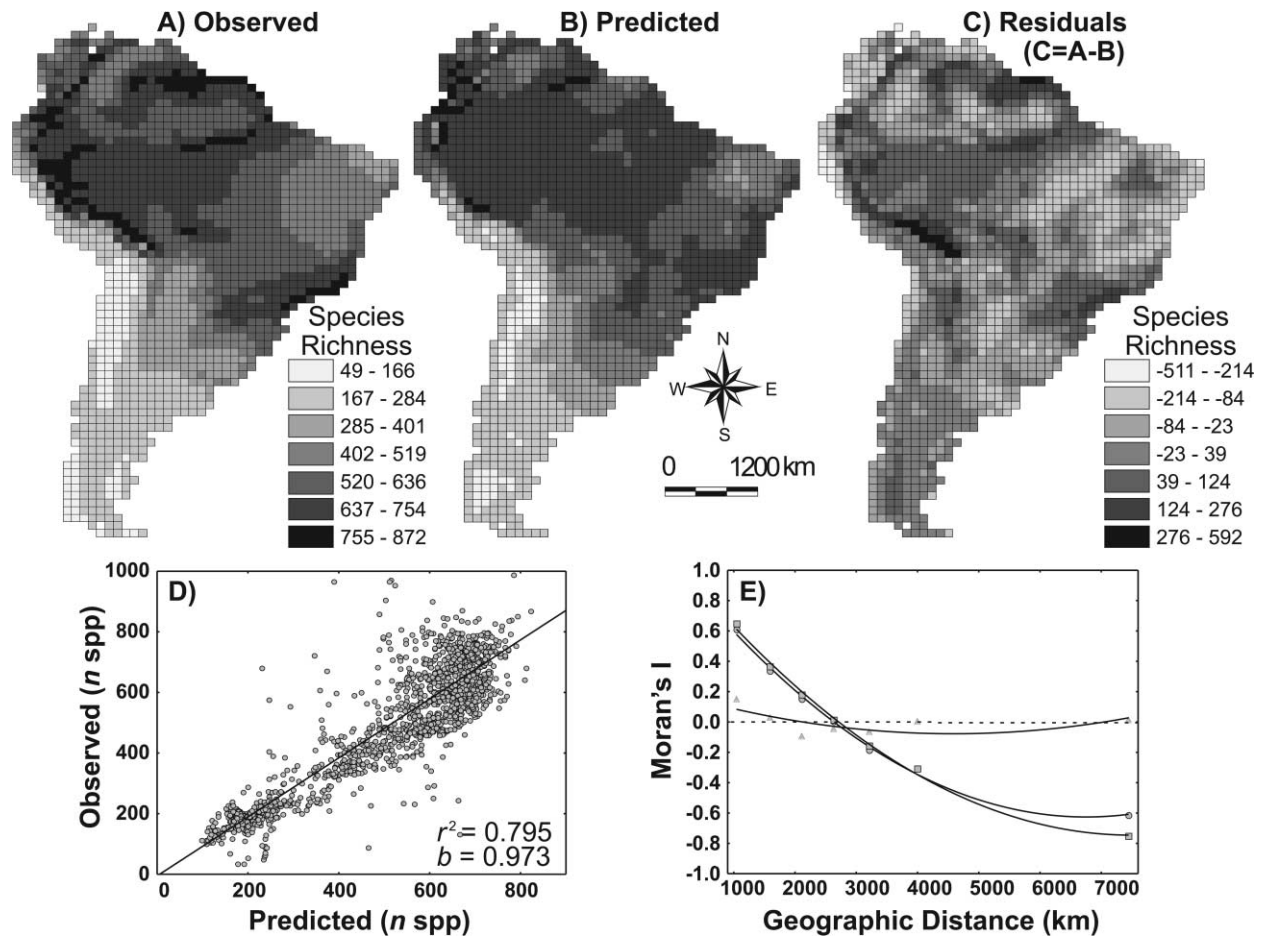


Figure 2: A, Observed spatial patterns in South American bird species richness. B, Best prediction of spatial patterns in South American bird species richness. C, Residuals of the regression of A against B, with coefficient of determination of 0.795, a slope of 0.973, and an intercept that does not differ significantly from 0. D, Relationship and regression fit between the patterns in maps in A and B; each point represents a map cell. E, Spatial autocorrelation of the patterns in the observed (A; squares), expected (B; circles), and residuals (C; triangles), showing the virtually complete lack of residual spatial autocorrelation.

Our model proved to have a high predictive power for the observed spatial patterns in species richness (fig. 2A, 2B). Indeed, most of the variation in the observed pattern was captured ($r^2 = 0.795$). Comparison of the maps in figure 2A and 2B shows that the model faithfully predicted the high bird richness in the Amazon and part of the Atlantic Forest as well as the low bird richness in the Caatinga and Atacama Desert. However, the model failed to accurately predict the high richness of the Andes and the southeast portions of the Atlantic Forest, as shown by the map of the residuals (fig. 2C). Except in those two biomes, there is only modest spatial autocorrelation in the regression residuals (fig. 2E), evidence that the model was able to predict all major spatial trends in species richness.

For the parameter combination that maximizes the predictive power of our model in terms of species richness,

the observed and predicted range size frequency distributions are also generally similar (fig. 3), although they differ in detail, as indicated by a Kolmogorov-Smirnov test ($D = 0.256$, $P > .05$). This difference is greater among small-ranged species; our model predicts fewer of those species than there are in nature. The predicted distributions tended to have more medium-large and fewer very small ranges than the observed distribution. Although most of the model's predictions are clearly right skewed regardless of the parameter combination, the model is not as good a predictor of RSD as it is of spatial patterns in species richness, as shown in figure 4B. Nonetheless, since we found a general similarity between observed and simulated RSDs, this second criterion for evaluation of model fit can be understood as an additional indicator of the structural realism of our model.

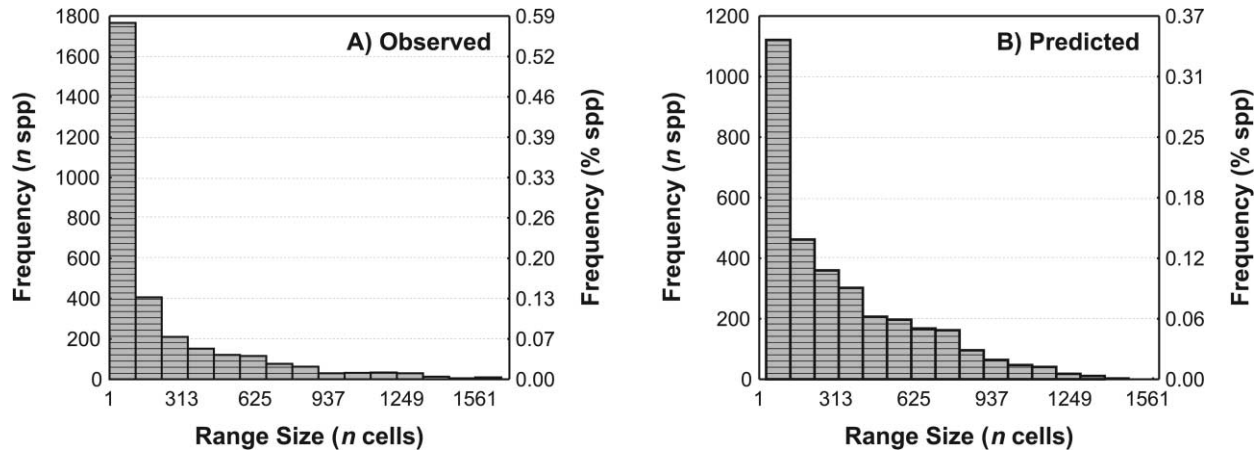


Figure 3: A, Observed range size frequency distribution. B, Predicted range size frequency distribution for the best model. Note that axis scales differ.

The model proved quite robust to small variations in model parameters, which may be an indication that the basic processes underlying the model successfully capture and predict the observed spatial patterns in species richness. Evidence for this robustness appears in the frequency distribution of measures of fit of spatial patterns in species richness and RSFD obtained for all explored parameter combinations (fig. 4). Despite the wide range of parameter space that was explored (see table 1), most parameter combinations generate models that provide good predictions of both species richness and RSFD. Correlation values (r_p) between observed and predicted spatial patterns in species richness ranged between 0.01 and 0.888 (median = 0.7323; fig. 4A), whereas the values of maximum unsigned difference between observed and predicted cumulative RSFDs (Kolmogorov-Smirnov D , which is 0 for perfect correspondence) ranged between 0.11 and 0.981 (mean = 0.4694; fig. 4B).

The predictions yielded by the best 25 parameter combinations (all with $r_p > 0.876$) provide not only strong correlations between observed and predicted spatial patterns in species richness but also quite accurate predictions of cell-by-cell magnitude of species richness. The regression coefficients of the 25 best models, spatially corrected by SAR when necessary, show that the mean (\pm SD) intercept value is -15.846 ± 28.396 , whereas mean slope value is 0.958 ± 0.093 . The 95% CIs of the intercept of 11 of the 25 best models bracket 0.0, whereas the 95% CIs of the slope of 22 models of 25 best models bracket 1.0.

The single factor with the most influence on the model's predictive power of spatial patterns in species richness was the parameter that regulates the conservatism of niche breadth (ω ; ANOVA F ratio = 205.858). Indeed, when

niche breadth is highly conserved over evolutionary time, the fit between predicted and observed patterns increases. The second most influential factor was extinction probability as a function of range size (α ; F ratio = 172.724). In our model, a low to medium extinction probability maximized model predictive power. The third and fourth most influential factors were the conservatism of niche center (Δ ; F ratio = 168.260) and the latitudinal position of the initial species (G_{lat} ; F ratio = 12.008). Predictive power of the model was maximized by high parameter values for conservatism of the niche center and by initial species starting at low latitudes. The parameter that regulates the niche breadth of the initial species was the last significant factor (σ ; F ratio = 8.495), whereas the longitude of the starting position of the initial species was not significant (G_{long} ; F ratio = 1.254). For further details on the relationship between the model parameters and the predicted spatial patterns in species richness, see figure B2 in the online edition of the *American Naturalist*.

Thus, our model suggests that richness patterns most like the observed patterns for South American birds are produced when niche evolution is strong enough to allow some lineages to adapt and disperse toward environmentally distinct regions (evolution of niche center) but weak enough that niche conservatism maintains most of descendant species close to the core diversification region, with niche breadths conserved. When the diversification process starts in the tropics, the tropics become the most species-rich region. In contrast, longitudinal position did not significantly affect model fit. In other words, when the initial species originates in a tropical region and niche conservatism exerts a strong but not overwhelming force, it prevents most species from reaching extratropical regions. Thus,

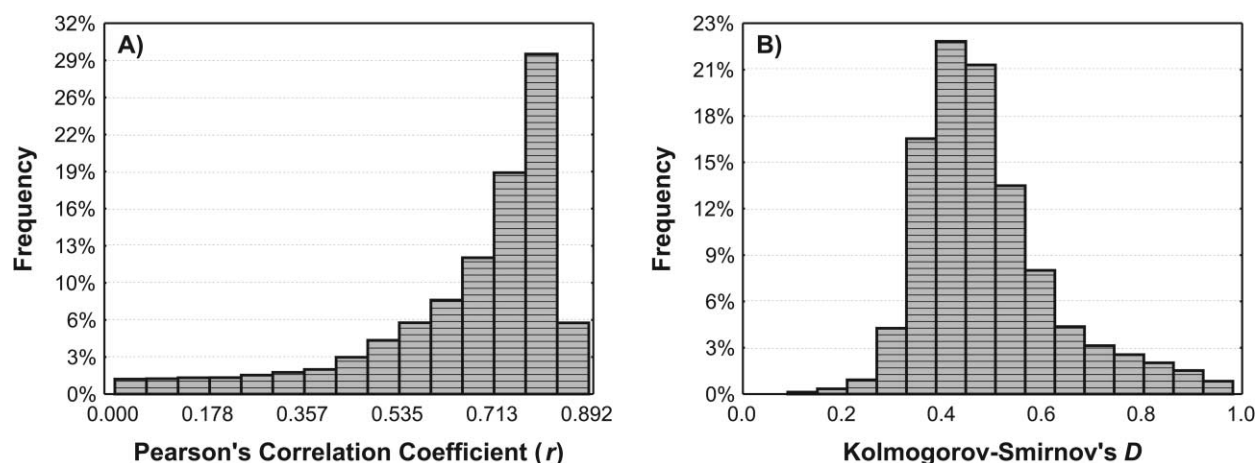


Figure 4: Frequency of values of (A) Pearson's correlation coefficient between observed and predicted patterns and (B) Kolmogorov-Smirnov D between observed and predicted range size frequency distributions. Data shown are results of simulations with all parameter combinations.

niche conservatism causes species to accumulate at lower latitudes and prevents most species from reaching higher latitudes, where they are poorly adapted to the environment. This process creates a geographical gradient in species richness that resembles the pattern observed in nature, and thus it increases model predictive power.

With regard to the predictions of the RSFD, the most important factor was extinction pressure as function of range size (α ; F ratio = 8,639.735); low extinction pressures maximized model predictive power. Just as for spatial patterns in species richness, conservatism of niche breadth (ω ; F ratio = 179.086) and center (Δ ; F ratio = 42.72) were also very influential for the RSFD predicted by the model. Niche breadth of the initial species was the next most important factor (σ ; F ratio = 39.283). Latitude of the starting position for the initial species was a marginally significant factor for the prediction of RSFD (G_{lat} ; F ratio = 2.819), whereas longitude was not significant (G_{long} ; F ratio = 0.745). For further details on the relationship between the model parameters and the predicted RSFD, see figure B3 in the online edition of the *American Naturalist*. In summary, the model yielded its maximum predictive power for RSFD when extinction pressure as a function of range size was weak, when both niche breadth and niche center tended to be conserved, and when the initial species had a narrow to medium niche breadth.

Discussion

The Role of Niche Conservatism and Niche Evolution in the Origin of Richness Gradients

This study yields an important result: an evolutionary model of niche dynamics that balances niche conservatism

and niche evolution, operating within a spatially heterogeneous, temporally fluctuating environment, seems to be sufficient to generate broadscale spatial patterns in species richness, on an environmentally heterogeneous map, that closely resemble the observed contemporary patterns. These findings are in accordance with recent theoretical and empirical advances in ecology and biogeography (e.g., Ricklefs and Latham 1992; Holt 1996; Prinzing et al. 2001; Stephens and Wiens 2003; Svenning 2003; Quian and Ricklefs 2004; Wiens 2004; Wiens and Donoghue 2004; Cardillo et al. 2005; Hawkins et al. 2005, 2006; Wiens and Graham 2005; Jablonski et al. 2006).

Over evolutionary timescales, shifting climatic factors change the environmental landscape in which the species are embedded (Dynesius and Jansson 2000; Jackson and Overpeck 2000; Jansson and Dynesius 2002; Ackerly 2003). If a species fails to respond, through range shift or adaptation (e.g., Davis and Shaw 2001), to the new environmental conditions to which it is subjected (Hoffmann and Blows 1994), climatic fluctuations may reshape the species' geographical range or eventually lead to range fragmentation and subsequent allopatric speciation (Wiens 2004) or even extinction (McDonald and Brown 1992). The failure of a species to adapt to the effects of environmental oscillations within its geographical range has been characterized as niche conservatism (Wiens 2004). Besides affecting range fragmentation, niche conservatism may also have contributed to shaping contemporary geographical gradients in species richness (Wiens and Donoghue 2004; Wiens and Graham 2005).

Because most major lineages may have originated in the tropics and were adapted to tropical climatic regimes, either lineages may have become extinct in regions in which

the climate changed from tropical to temperate (Hawkins et al. 2006) or no founder species may have successfully adapted to nontropical climatic regimes (Wiens and Donoghue 2004). In this study, our simulation model allowed us to evaluate whether niche conservatism may have contributed to the creation of the observed spatial patterns in species richness. By modeling the degree of niche conservatism (niche heritability) as a variable parameter of the model, we were able to simulate conditions of strong niche conservatism or rapid niche evolution. Our model has shown that if niche conservatism prevails over niche evolution and if the diversification process is driven by range fragmentation, descendant species tend to accumulate in regions of similar environmental characteristics, which are usually geographically close to the zone of origin of the clade. As a consequence, when we simulate a condition in which a lineage has originated in the tropics, our simulation model yields predictions that closely match the observed spatial patterns in species richness (the “out of tropics” model; Jablonski et al. 2006; Diniz-Filho et al. 2007).

Notice that in our model the degree of niche conservatism is not independent of other parameters of the model, especially geographic range size. The shift in species’ niche center in relation to the extrinsic change in environmental conditions is the best way to characterize the degree of conservatism in a phylogenetic context (i.e., ancestor-descendent relationship for a given species’ trait). In our simulations, because isolated populations arise from fragmentation of the ancestral species’ geographic range, confined by the limits of their niche to “habitat islands,” the niche center of the descendant species will always be within the niche breadth of the ancestor species. Thus, niche conservatism will tend to be stronger for small-ranged species, in which distances between ancestor and descendent niche centers will generally be low, even when the niche center is allowed to shift toward a new environmental condition. Indeed, recent studies using comparative methods at the species level showed a stronger phylogenetic signal of range sizes for small-ranged species than for large-ranged species (Jones et al. 2005).

Finally, it is worth noting that our simulations were targeted to match patterns of species richness defined by a relatively coarse-grained data set, although more detailed data sets exist (Rahbek 1997). However, considering the overall strong correspondence between the patterns recovered by fine-resolution data sets and the database we used, it is unlikely that our broadscale simulations are qualitatively affected by minor, scale-dependent problems in data resolution (Mathias et al. 2004).

Environmental Fluctuations, Niche Dynamics, and Range Shifts

Climate change dynamics exert a strong influence on species’ geographical ranges (e.g., Dynesius and Jansson 2000; Jackson and Overpeck 2000; Davis and Shaw 2001; Ackerly 2003; Parmesan and Yohe 2003; Davis et al. 2005). Species’ range boundaries in nature fluctuate greatly over time, driven either by environmental changes or by niche shifts resulting from evolutionary, ecological, or demographic forces (e.g., MacArthur 1972; Kirkpatrick and Barton 1997; Ackerly 2003; Gaston 2003; Holt 2003). Because no time series for paleoclimate data are yet available, in our model climate fluctuations are implemented as simple sine waves. Indeed, it is well known that the magnitude of climatic fluctuations has varied greatly, from several degrees Celsius within a few decades to virtually no climate change over a millennium. However, although a precise sine wave pattern of fluctuation may not be the rule in nature, roughly cyclic changes in temperature and humidity may have occurred commonly, over various timescales (e.g., Webb and Bartlein 1992; Dynesius and Jansson 2000; Rind 2000; Kukla et al. 2002).

In our model, climatic fluctuation triggers biogeographical events at the species level, causing species’ geographical ranges to contract, expand, fragment, or undergo extinction. Indeed, it is expected that such events may happen as a consequence of any climatic fluctuation over sufficiently broad spatial and temporal scales. Although we agree that model realism would be enhanced by using actual time series of paleoclimate data, we believe that the sine wave fluctuations implemented here represent the most realistic general pattern that one can extract from the broadscale patterns of incomplete paleoclimate data that are available. However, the main weakness of this approach is the lack of a realistic timescale in the simulation, which does not allow us to infer anything about the relationship between climatic fluctuation and diversification rate of birds in South America. However, the model developed here seems to be robust to this lack of information because it reproduces the observed patterns after a given number of species is achieved, as observed for real bird data. In fact, after the model reaches about 1,000 species, the spatial pattern in species richness remains constant over time. Moreover, diversity gradients in South America are similar for other groups with large numbers of species (Bini et al. 2004), suggesting that taxon-independent processes drive such patterns.

Direct and Indirect Effects of Environment on Richness Gradients

As expected, the environmental variables used in the model can explain part of the variance of observed spatial patterns

in species richness. Using all six environmental variables as predictors of observed spatial patterns in a multiple regression analysis, we found that 75.6% (r^2) of continental patterns of bird species richness was explained by environment, a magnitude of explanation close to levels found in most correlative studies (e.g., Hawkins et al. 2003b). Thus, one could argue that the predictive power of our model is actually driven indirectly by the environmental variables that we used to characterize landscape patterns in South America and that the model dynamics should therefore not be interpreted as adding substantial information. However, our model achieves its maximum predictive power using only minimum and maximum annual temperature and humidity. In a traditional multiple regression, with species richness as response variable and only these four factors as explanatory variables, only 62.6% (r^2) of the variance in species richness of birds in South America is explained, as opposed to 79.5% explained by our model, using only those environmental variables. However, these coefficients are difficult to compare because of different parameterization approaches between the statistical analysis and the simulation model. Nevertheless, this contrast suggests that in addition to incorporating explicit biogeographical and evolutionary mechanisms, the model performs better than corresponding correlative models, at least for South American birds. Although useful, correlative studies lack the theoretical basis to explain how these environmental variables drive spatial patterns in species richness in evolutionary terms (Currie et al. 1999, 2004).

Our model introduces a conservative analytical framework in which its predictions were statistically analyzed under a robust methodology, testing not only the overall agreement of spatial patterns in species richness but also the accuracy of the predictions for richness patterns (i.e., the intercept and slope of the regression) and for the similarity of the modeled range size frequency distributions to the observed ones. In spite of the overall success of the model, it is important to highlight that it failed to predict patterns of extreme species richness along the Andes and in the Atlantic Rain Forest. This failure is probably due to historical contingencies and geographically local components of diversification that were not captured by our model. For example, in the case of the Andes, many studies have shown the effects of altitudinal gradients and habitat heterogeneity on diversity, which in turn create more complex patterns of evolutionary diversification at local scales (Rahbek 1997; Ribas et al. 2005; Weir 2006). Model predictive power in the Andes might be increased by incorporating particular historical events and their effects at local spatial scales. Of course, the next step is to test the model's predictive power for other biogeographical patterns (e.g., beta diversity, endemism), for other taxa (e.g.,

mammals, amphibians, and trees), and in another domains (e.g., sub-Saharan Africa, North America).

We emphasize that under the processes simulated here, the model does not use any quantitative assessment of environmental variables to control diversification; the probabilities of speciation and extinction do not vary with a species' position in niche space or with its geographical location. For this reason, the high correlation between predicted and observed richness patterns can be viewed as an indirect effect of evolutionary history rather than a direct effect of climate driving species richness (see next section). This view leads us to the conceptual distinction between cause and correlation (see Shipley 2002), a distinction more clearly seen when we consider that the environmental conditions in the region where the lineage originated have a strong effect on the shape of the spatial patterns in species richness. These conditions define the optimal environmental condition of the initial species. This means that if one lineage originates in the cold, dry, unproductive region of the Atacama Desert, for example, and niche conservatism is sufficiently strong, it is likely that the model will predict this region to be particularly rich in species. Indeed, the ecological zone of origin of the lineage is a very important factor driving model predictions, as conjectured by historical biogeographers since Buffon and de Candolle (Lomolino et al. 2005).

Ancestral Conditions and Niche Dynamics

The mechanisms that promote niche conservatism cannot be considered absolutely random with respect to ancestral niche center and breadth. Although in our model speciation is equally likely to occur anywhere in a species geographic range, extinction would tend to be more frequent in regions of extreme environmental conditions (e.g., very high or very low temperature). For example, if a species has its fundamental niche center near the highest condition of a given environmental variable (i.e., temperature) and this environmental variable oscillates (e.g., decreasing temperatures throughout the domain), the species' realized niche (as expressed in its range size) would be more adversely affected than that of another species with its niche center at intermediate environmental conditions. The latter species would be able to track changed environmental requirements across the geographical space, regardless of the direction of the shift of the environmental variable (Davis and Shaw 2001; Davis et al. 2005). Clearly, final geographical patterns in species richness in the model are dependent not only on climate change but also on the particulars of the ancestral condition and species responses in ecological time (e.g., spread into suitable, contiguous environments) and/or evolutionary time (e.g., adaptation to new or changed environmental conditions).

In our simulations, the map location where the lineage originates was chosen at random in order to study the response of niche dynamics to different initial environmental conditions for the origin of the clade. However, under a biogeographically more realistic approach, one might apply the niche dynamics model to spatial patterns in species richness for a small lineage or clade (or separately for a set of related clades) that has a well-known center of origin (e.g., Bjorholm et al. 2006). Also, by comparing niche centers of phylogenetically related species within the selected group or disjunct lineages with intercontinental distributions, it should be possible to estimate the magnitude of evolutionary divergence (or niche conservatism) from a common ancestor, which would lead to a more specific test of our simulation model (Ricklefs and Latham 1992; Peterson et al. 1999; Ackerly 2003; Ricklefs 2006). Thus, after defining a specific geographical or ecological zone of origin and specifying niche characteristics and the magnitude of niche conservatism over time, one can evaluate the correlation between predicted and observed spatial patterns in species richness. We expect that model parameterization based on observed phylogenetic and biogeographical data may decrease the need for exploring a wide scope of parameters and substantially improve the model's predictive power.

Concluding Remarks

Further simulation studies could implement more realistic models, including habitat choice, dispersal patterns through time (Holt 2003), species interaction and consequences of niche overlap (Case and Taper 2000), gene flow within and between range fragments (Kirkpatrick and Barton 1997), population and metapopulation dynamics (Hanski 1998), the genetic basis of speciation (e.g., Gomulkiewicz and Holt 1995; Gavrilets and Vose 2005), multiple colonization events or more than one lineage evolving simultaneously, and empirical dynamics of climate change and its effects on species' geographical ranges (Dynesius and Jansson 2000; Jackson and Overpeck 2000; Jansson and Dynesius 2002; Ackerly 2003). However, each of these thrusts toward increased realism would lead to much more complex models, and it is likely that the results of such models would become quite difficult to interpret and evaluate with respect to the relative importance and role of model parameters. Although it is difficult, at present, to evaluate this particular problem of model complexity, we hope that our model falls well within the "Medawar zone" (Grimm et al. 2005), in which model design includes some sacrifice of biological realism for the sake of general interpretation of model results that can be projected in different scales and hierarchical levels, instead of very specific and realistic models that require cumbersome and possibly prohibitive analytical procedures.

Our niche dynamics model is an attempt to merge, in a spatially explicit context, several widely accepted evolutionary, biogeographical, and ecological mechanisms, together with recently developed ideas on niche conservatism and evolution. We found that it is likely that niche conservatism has played a role in shaping these patterns, and indeed, our model has strong and accurate predictive power of observed spatial patterns of South American birds. We do not claim that the validity of our results and interpretations are based on the materiality (i.e., obtained by hands-on experiments) of our study (Sismondo 1999), but validity is based instead on the close connection between our model and (1) the underlying scientific theory that supports this study, (2) the accuracy and fidelity of the model-building techniques we employed, (3) the observed data for the geographical distribution of birds, (4) the pattern-oriented approach used to parameterize the model, (5) the stability and robustness of our model in relation to parameter variation, (6) the strength of the statistical inference procedures used, and, most important, (7) the power of the model to predict observed patterns. Finally, we agree with Wiens and Donoghue (2004) that ecology and historical biogeography have much to offer each other, and we hope this article will motivate researchers to study spatial patterns in species richness under an integrated theoretical and methodological framework.

Acknowledgments

We thank (alphabetically) D. Ackerly, M. Bini, N. Gotelli, C. Rahbek, J. Wiens, M. Willig, R. Whittaker, and an anonymous reviewer for useful suggestions on earlier versions of the manuscript. T.F.L.V.B.R. also thanks W. Martins for the useful suggestions on the design of a grid computing platform. Biological data were provided by NatureServe in collaboration with R. Ridgely, J. Zook, the Nature Conservancy, Conservation International, World Wildlife Fund, and Environment Canada. T.F.L.V.B.R. is supported by a Fulbright/Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) fellowship (15061630-2668/05-0), by the National Science Foundation (NSF), and by the University of Connecticut. J.A.F.D.-F. has been continuously supported by several CAPES and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) fellowships. R.K.C. was supported by the NSF (DEB-0639979) during this study.

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