ENVIRONMENTAL GRANULARITY, RIVERS AND CLIMATE HISTORY AS SHAPING FACTORS FOR SPECIES' DISTRIBUTION AND DIVERSITY PATTERNS

BY

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CHAPTER 1

The environmental landscape and its influence on species' distributional

patterns

ABSTRACT

Several mechanisms are involved in shaping species' distributions, such as abiotic

parameters of climate and substrate; biotic interactions with competitors, predators,

and mutualists; and geographic considerations that constrain dispersal. Janzen, in

1967, proposed that mountain passes are effectively higher in the Tropics than in

temperate areas in terms of their effectiveness in limiting dispersal, creating greater

opportunity for isolation of populations, and differentiation into new species. Here, I

analyze quantitatively predictions derived from Janzen's theory via 1000 virtual

species across South America covering all major environments on the continent,

taking into account effects of environmental contiguity and connectivity, effects of

seasonality, and presence of known biogeographic barriers (rivers, principally).

Virtual species' distributions were obtained by calculating Euclidean distances in

ecological space to 1000 seed points, and applying different thresholds of ecological

similarity within which the species is allowed to disperse into adjacent pixels.

Distributional areas were measured taking into account only mean environmental

similarity across the year, and considering the effects of seasonality and known

geographic barriers. The results illuminate the situation: distributional areas are

smaller in temperate areas when only mean similarity is considered (contra Janzen),

but the pattern reverses when seasonality and barriers are considered, confirming and clarifying Janzen's ideas regarding generation of greater biological diversity in tropical areas as compared with temperate areas.

Keywords: landscape subdivision, species' distributions, biogeography, virtual species

INTRODUCTION

The species numbers of a particular site, often termed α-diversity, can be measured as the number of species whose distributions overlap (Brown 1995; MacArthur 1972). Species are present in areas where sets of biological, abiotic, and historical factors coincide in being favorable for colonization and persistence (Grinnell 1914; Grinnell 1917; Hutchinson 1957; Soberón and Peterson 2005). Global patterns of distribution of biodiversity have been explored considerably, documenting greater diversity in tropical areas than at higher latitudes, which has been explained by several theories attributing causal roles to environmental heterogeneity (MacArthur and Wilson 1967; Tews et al. 2004), system energy (Hawkins et al. 2003a; Hawkins et al. 2003b), history (Hawkins et al. 2003b), and latitude (Pianka 1966; Rapoport 1982).

Janzen (1967) proposed a mechanism by which environmental contiguity and associated discontinuities (distributional barriers) might structure species to produce such diversity patterns. Under these ideas, tropical mountain passes represent stronger barriers to species than temperate mountain passes owing to differential

physiological adaptation of species to environments (Ghalambor et al. 2006; Janzen 1967; Kozak and Wiens 2007). Tropical species will face a stronger barrier since temperature variation through the year is narrow and steady, while at higher latitudes such regimes are broader, and overlap between lowland and highland temperature ranges is more common. These ideas suggest that species adapted to seasonally fluctuating conditions in temperate regions could encounter less trouble with dispersing across mountain passes that might constitute barriers to tropical species.

As a result of the relative environmental homogeneity of conditions in the Tropics across the year, species in this area are expected to have narrower environmental tolerances, while temperate species must adapt to broader environmental ranges, given the diversity of conditions they experience through the course of a year (Ghalambor et al. 2006; Janzen 1967). Thus, one key prediction of Janzen's theory is that tropical species will have more restricted distributional areas, while temperate species will have broader distributional areas.

Real species' distributions are subjected to diverse, interconnected processes, which complicates any effort to separate them (e.g. biological interactions, abiotic requirements, environmental landscape, sampling biases, taxonomic discrepancies). As a consequence, their individual input into shaping species' distributions becomes difficult to discern. Artificial species (Austin et al. 2006; Jiménez-Valverde and Lobo 2007), which can be "created" under controlled and known parameters, allow investigators to test effects of particular parameters of interest.

In the present analysis, I (1) tested effects of environmental specificity on geographic range size via creation of artificial species with different degrees of environmental

specialization, (2) measured fragmentation of suitable areas for these species owing to topographic barriers (elevation and rivers), and (3) tested the effect of seasonality on geographic range sizes in South America across a dramatic tropical-to-temperate gradient.

METHODS

Study area.- The study covered all of South America, including the southern extreme of Central America (Figure 1A), an area comprising high-latitude temperate climates in the south, hot and dry conditions in the Atacama Desert region, tropical rain forest in the Amazon Basin, and Mediterranean climates in southern Chile, among others. Important topographic features include the Andean mountain chain that spans South America from north to south, the Amazon forest in the north, and several biomes considered global biodiversity hotspots (Mittermeier et al. 1998; Myers 2003; Myers et al. 2000): the tropical Andes, the southeastern Brazilian Atlantic Forest, the Tumbés-Chocó-Magdalena region, and the Chilean Valdivian forest.

Environmental data.- In recent years, large quantities of climatic data have been made available (Hijmans et al. 2005), permitting rich characterization of environmental landscapes. To avoid overparameterizing this space, I used seven variables from WorldClim's bioclimatic dataset (annual mean temperature, mean diurnal range, maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation of the wettest quarter, precipitation of the driest quarter and precipitation seasonality) known to be relatively uncorrelated (Peterson

and Nakazawa 2008) in raster format at a spatial resolution of 2.5' (Hijmans et al. 2005). These maps of environmental conditions were reprojected into an Albers projection (SAD 1969 Albers), using the South American datum 1969 (central meridian -60º; standard parallels -5º and -42º; and latitude of origin -32º), to allow consistent area calculations. These variables were used to create a seven-dimensional environmental space to describe ecological variation across the study area. Four environmental datasets, consisting of monthly means of temperature and precipitation and minimum and maximum temperatures for January, April, July and October, were constructed at the same spatial resolution and geographic projection to permit incorporation of seasonal environmental variation.

In a separate, vector-based dataset, I included rivers known to constitute major barriers to species' distributions; I used bird species to select these rivers owing the relatively complete knowledge of their taxonomy and distributions. Rivers included the Amazon, Marañón, Ucayali, Solimões, Madre de Dios, Madeira, Purus, Juruena, Negro, Tapajós, Xingú and Magdalena (Figure 1A). These "barriers" were used to constrain dispersal by virtual species (see below).

Virtual Species.- Using Hawth's Analysis Tools (Beyer 2004) for ArcGIS 9.2, I selected 1000 sites at random within South America (Figure 1B); these locations were used as seed points for creating virtual species. I simulated introduction of a virtual species at each point, and allowed it to spread to environmentally similar but contiguous areas. Environmental similarity was summarized as the Euclidean distance from the seed point to every other cell in the seven-dimensional environment space. I created species based on 7 thresholds of environmental

similarity representing different levels of specialization: 99.0%, 97.5%, 95.0%, 92.5%, 90.0%, 80.0% and 50.0% of the full distributions of similarity values across South America; that is, for the first threshold, I identified the 1% of the cells that were most similar environmentally to the point (Figure 1C). As a result, I created 7000 virtual species, one for each seed point X similarity threshold combination, with good representation of the geography and environmental heterogeneity of the continent, and with diverse levels of environmental specialization.

To incorporate seasonality considerations, I calculated Euclidean distances from each seed point to all cells in the study area (as above) for each of the four seasonal datasets separately. This process produced four distance maps corresponding to each season for each seed point. These maps were summarized as the minimum distance (i.e., maximum similarity) from every cell in any of the four seasons to the corresponding seed point. Finally, the minimum distance maps were submitted to the same threshold-based classification process described above.

Proportional habitable area (PHA).- Environmental combinations are represented in different concentrations across landscapes (Soberón and Peterson 2004). For this reason, a measure of the proportional habitable area for the species, regardless of connectivity to the starting point, indicates the relative representation of habitable areas across the continent for a species. I calculated PHA as the ratio between the area selected as suitable and the total study area after applying each ecological similarity threshold (Figure 1C inset).

Proportional patch area (PPA).- Although virtual species' distributional areas were determined by selection of environmentally similar pixels in the seven-dimensional

space, their spatial representation includes disjunct patches of suitable conditions. Hence a useful indicator of fragmentation of suitable areas is the size of the patch (i. e., number of interconnected pixels considered habitable for the species) in which the seed point lies (Figure1C inset). Patch areas were measured under each threshold, and divided by the total study area. These parameters were calculated individually at each similarity threshold.

PPA calculations were repeated for four combinations of seasonality and inclusion of barriers (rivers): (a) no geographic barriers and no seasonality considered; (b) geographic barriers but no seasonality; (c) seasonality but no geographic barriers; and (d) both geographic barriers and seasonality. Barriers were included simply as discontinuities within otherwise continuous potential distributional areas; seasonality was based on the maximum similarity across the four seasons.

PPA values for each seed point were imported into into ArcMap 9.2 and an interpolated surface using these values was created for visualization purposes for each of the barrier-seasonality combination using the inverse distance weighted (IDW) method with a power of two and considering the twelve closest neighbors. Correlations between PPA/PHA ratio values and latitude and longitude for all similarity threshold values were also calculated to test for the influence of these geographic variables (latitude and longitude) on environmental fragmentation. Finally, a two-way ANOVA, testing the effects of seasonality and barriers (individually and in tandem) on PPA/PHA ratio values was performed at each of the seven similarity thresholds.

RESULTS

Virtual species varied from very narrow (restricted range) to very broad in their distributions. The highest values of specialization (similarity threshold = 99%) for all analysis created very restricted distributions for the virtual species (Figures 2 and 3), so the individual effects of seasonality and barriers were better appreciated at medium-to-low similarity thresholds.

Virtual species with distributions produced without consideration of seasonality and barriers showed that contiguous suitable environments for very specialized species can be restricted in extent (Figure 2). However, species in northern and central South America could occupy high proportions of the total habitable area (Figure 2), and range restriction was observed only in the extreme south. As the similarity threshold was lowered, PPA values approached PHA values as a result of greater connectivity for broader tolerance by the species. Under these assumptions, consequently, species in the Andes, particularly at the southern end, showed smaller distributional areas (Figure 2).

If seasonality was considered, species showed broader distributional areas at all similarity thresholds, relative to species produced without considering seasonality. Restricted-range species were obtained only for specialized species (Figure 3), and were concentrated in northern South America. Less restricted species occurred from the southern part of the Amazon Basin south to the southern tip of South America, especially in the Andes (Figure 3). Broad distributional areas and high connectivity was observed for all species in comparison with analyses that did not take seasonality into account.

Finally, inclusion of riverine barriers in the analyses produced more fragmented distributional areas in the Amazon region (Figures 2 and 3) and northern South America in general, compared to species created without barriers. The role of rivers in shaping species' distributions is particularly evident in the non-seasonality analysis with lower similarity thresholds (Figures 2 and 3 and Table 1).

Correlations between PPA/PHA and longitude and latitude produced similar results (Table 1).Values for latitude (most interesting to the Janzen ideas) were positive when seasonality and barriers were not considered, and negligible when only seasonality was considered; when barrier effects were included, they became strongly negative. The ANOVA indicated significant effects of and their interaction of seasonality and barriers in essentially all cases.

DISCUSSION

The use of virtual species in these explorations merits some discussion. Calibration of the effects of different factors (e.g., barriers) in terms of real area reduction of species' ranges of course depends on our artificial thresholds, and as such does not allow direct comparisons. However, only with virtual species developed with explicit ecological niche breadths and limiting factors was I able to develop the inferences presented herein.

Lower fragmentation in tropical zones observed in my non-seasonal analysis without barriers results from greater contiguity among similar environments in these areas, so species occupy higher proportions of their habitable areas than do species in

temperate and highland areas. This pattern results from the use of mean values of environmental variables with similar values across broad lowland areas, opposite to what is expected in the highlands, where environments are interrupted by mountain tops and valleys. Table 1 shows correlation values between the PPA/PHA ratio and longitude and latitude at all similarity thresholds. Most correlations are < 0.5, except for those between similarity thresholds of 50% and 80% and latitude, which are the highest values obtained: 0.600 and 0.779, respectively.

The geographic distribution of PPA values when seasonality was considered corresponds much better to predictions derived from Janzen's ideas, with species showing reduced distributional disequilibrium in temperate areas, and those species with more restricted distributional areas species in tropical areas (Figures 2 and 3). This pattern reflects the seasonal "experience" of changing conditions compared to those in the Tropics, and how it is reflected in broader colonization potential, one of the important ideas in Janzen's theory. Inclusion of geographic barriers further fragmented tropical species' distributions in both seasonal and non-seasonal analyses. However, the effect of inclusion of these barriers was most evident in non-seasonality analyses, which suggest interactions between the sets of effects as shown by the ANOVA analysis (Table 1).

In general, Janzen's (1967) ideas were supported amply by my analyses: geographic barriers influence the temperate-tropical balance in species' distributions, but only analyses incorporating seasonal considerations could replicate the tropical fragmentation predictions fully. However, because river barriers refined patterns observed in the tropical lowlands, interactions between environmental stability and

physical barriers may produce the patterns that Janzen attempted to explain. The roles of these two factors may vary depending on the geographic region, so replication of analyses on other continents may be informative.

Ghalambor *et al.* (2006) described a test of Janzen's hypothesis using models that integrated operative models in which environment drives population energetic and dynamics determining potential distribution of species. Based on Janzen's hypothesis, range-restricted species concentrate at lower latitudes. The methodology I used produces potential distributions based on of a set of climate variables, while the analysis of Ghalambor *et al.* (2006) was based only on temperature. In spite of these differences in methodology, both sets of results were similar and consistent with Janzen's predictions.

Ghalambor *et al.* (2006) identified latitude and seasonality as factors influencing between-elevation climate overlap. Although I did not test for climate overlap in particular, the importance of seasonality in shaping species' ranges is evident from comparing models with and without seasonal considerations. The distributional pattern of PPA values across the continent (a) shows a marked regionalization that contradicts the latitudinal gradient idea; (b) may be indicative that environmental structures vary from biome to biome; and (c) could influence speciation rates, making some regions more adequate for speciation than others which, over long periods of time, could produce patterns of biodiversity (Kozak and Wiens 2007). Reconstructions of past climates and the study of their evolution through time can be used for the interpretation of speciation processes and present patterns of biodiversity.

ACKNOWLEDGENTS

LITERATURE CITED

Austin, M. P., L. Belbin, J. A. Meyers, M. D. Doherty, and M. Louto. 2006. Evaluation of statistical models used for predicting plant species distributions: Role of artificial data and theory. Ecological Modeling 199:197-216.

Beyer, H. L. 2004.Hawth's Analysis Tools for ArcGIS, version 3.26.SpatialEcology.com.

Brown, J. H. 1995. Macroecology. Chicago, University of Chicago Press.

Ghalambor, C. K., R. B. Huey, P. R. Martin, J. J. Tewksbury, and G. Wang. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. Integrative and Comparative Biology 46:5-17.

Grinnell, J. 1914. Barriers to distribution as regards birds and mammals. American Naturalist 48:248-254.

—. 1917. The niche-relationships of the California thrasher. Auk 34:427-433.

Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J.-F. Guégan, D. M. Kaufman, J.
    T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, E. E. Porter, and J. R.
    G. Turner. 2003a. Energy, water, and broad-scale geographic patterns of
    species richness. Ecology 84:3105-3117.

Hawkins, B. A., E. E. Porter, and J. A. F. Diniz-Filho. 2003b. Productivity and history
    as predictors of latitudinal diversity gradient of terrestrial birds. Ecology
    84:1608-1623.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very
    high resolution interpolated climate surfaces for global land areas.
    International Journal of Climatology 25:1965-1978.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on
    Quantitative Biology 22:415-427.

Janzen, D. H. 1967. Why mountain passes are higher in the Tropics. American
    Naturalist 101:233-249.

Jiménez-Valverde, A., and J. M. Lobo. 2007. Threshold criteria for conversion of
    probability of species presence to either-or presence-absence. Acta
    Oecologica 31:361-369.

Kozak, K. H., and J. J. Wiens. 2007. Climatic zonation drives latitudinal variation in
    speciation mechanisms. Proceedings of the Royal Society B 274:2995-3003.

MacArthur, R. H. 1972. Geographical Ecology. New York, Harper & Row Publishers.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography.
    Princeton, Princeton University Press.

Mittermeier, R. A., N. Myers, and J. B. Thomsen. 1998. Biodiversity hotspots and major tropical wilderness areas: Approaches to setting conservation priorities. Conservation Biology 12:516-520.

Myers, N. 2003. Biodiversity hotspots revisited. BioScience 53:916-917.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853-858.

Peterson, A. T., and Y. Nakazawa. 2008. Environmental data sets matter in ecological niche modelling: and example with *Solenopsis invicta* and *Solenopsis richteri*. Global Ecology and Biogeography 17:135-144.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: A review of concepts. American Naturalist 100:33-46.

Rapoport, E. H. 1982. Areography: Geographical strategies of species. Oxford, Pergamon Press.

Soberón, J., and A. T. Peterson. 2004. Biodiversity informatics: managing and applying primary biodiversity data. Philosophical Transactions of the Royal Society of London Series B 359:689-698.

—. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics 2:1-10.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity: The importance of keystone structures. Journal of Biogeography 31:79-92.
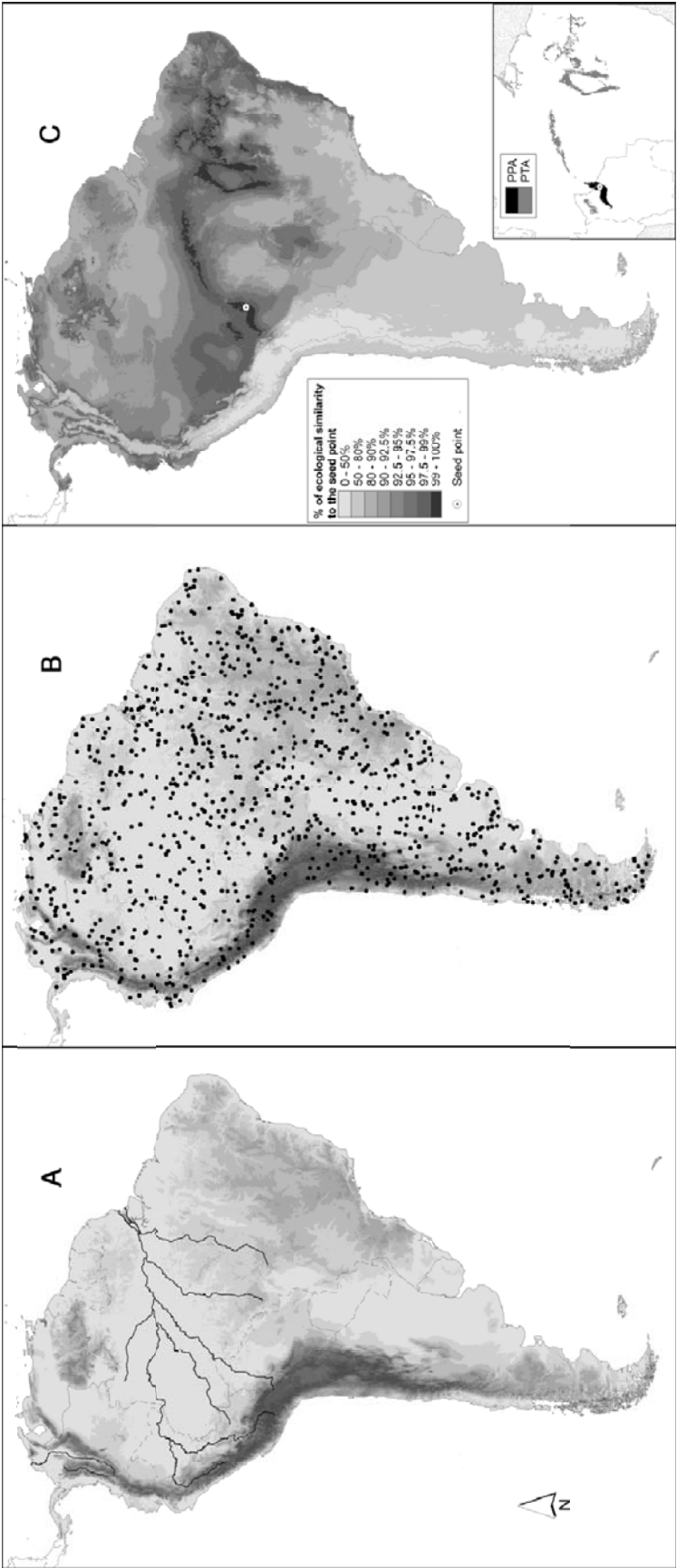
Table 1. Correlation values between latitude and longitude and Proportional Patch Area/Proportional Habitable Area (PPA/PHA) values calculated at the seven environmental similarity thresholds for all four combinations of seasonality and inclusion of barriers. P-values resulting from the two-way ANOVA tests for the effect of barriers (B), seasonality (S), and the interaction of these two factors (B x S) on PPA/PHA.

Similarity	No barriers No seasonality		Barriers No seasonality		No barriers Seasonality		Barriers Seasonality		Two-way ANOVA P-values		
Threshold	Longitude	Latitude	Longitude	Latitude	Longitude	Latitude	Longitude	Latitude	B	S	B:S
50%	0.3426	0.4824	0.2228	-0.6005	0.0742	0.0765	0.0700	0.0276	<0.001	<0.001	<0.001
80%	0.1763	0.2002	0.1725	-0.7793	0.1752	0.2014	0.2583	-0.0523	<0.001	<0.001	<0.001
90%	0.3257	0.4278	0.3519	-0.4496	0.2617	0.0799	0.3527	-0.2259	<0.001	<0.001	<0.001
92.50%	0.4028	0.3924	0.3829	-0.2853	0.2915	0.0503	0.3394	-0.3177	<0.001	<0.001	<0.001
95%	0.4480	0.3041	0.3375	-0.1753	0.3379	0.0083	0.3588	-0.3944	<0.001	<0.001	0.2625
97.50%	0.2301	0.2204	0.1474	-0.1235	0.3579	-0.1099	0.3144	-0.4176	<0.001	<0.001	<0.01
99%	-0.0378	-0.0578	-0.0529	-0.2105	0.2401	-0.1385	0.1391	-0.4958	<0.001	<0.001	<0.001

Figure 1. A. Study area: South America and rivers considered to constitute biogeographic barriers, shown overlain on elevation. B. Random points used as seed points for creation of virtual species, shown overlain on elevation. C. Environmental similarity patterns for a point in southern Brazil, and in the inset 99% thresholding to show PPA (gray) and PHA (black).
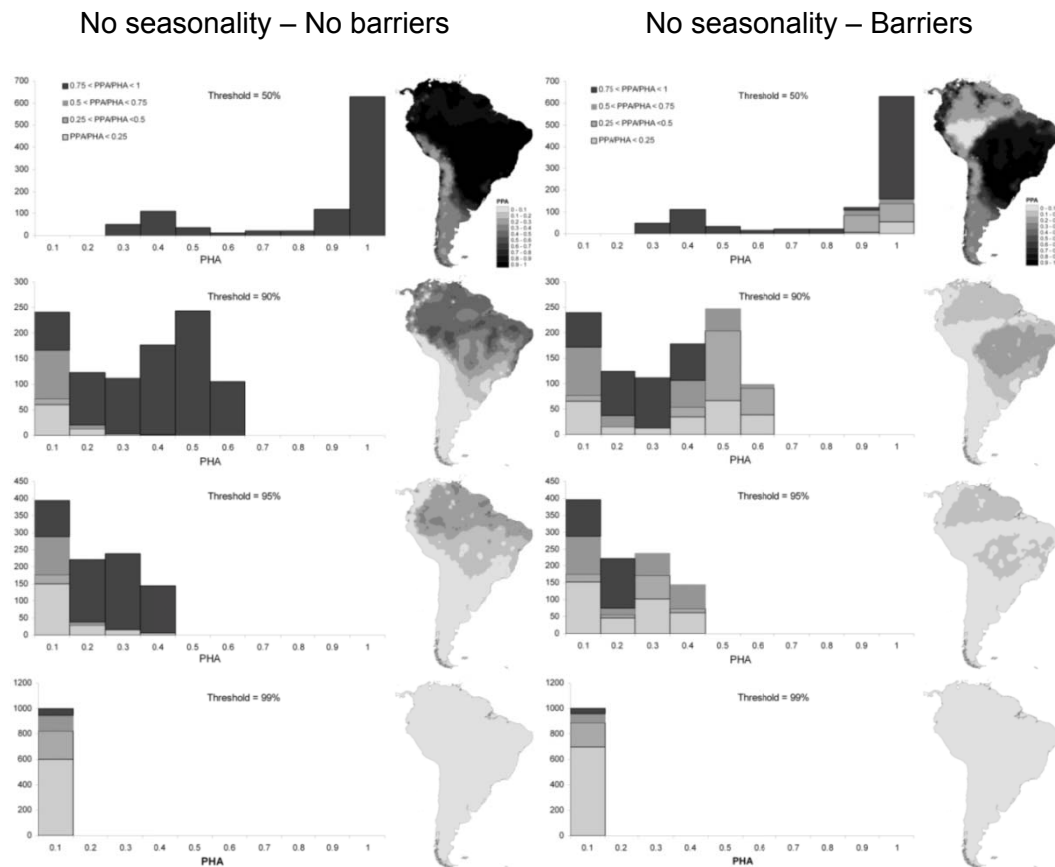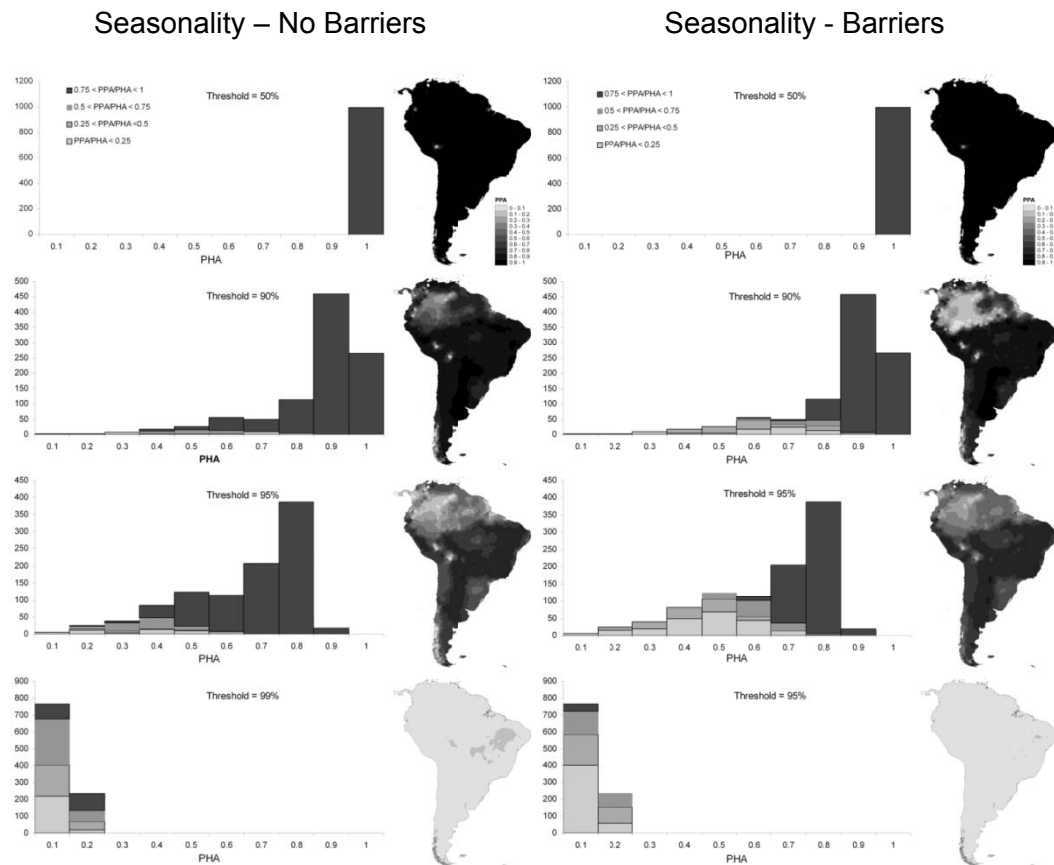
Figure 2. Interpolated maps from Proportional Patch Area (PPA) values using Inverse Distance Weighted (IDW) method for the no-seasonality analysis without (left) and with (right) the inclusion of barriers (rivers); gray tones correspond to the size of the areas produced at each seed point from narrow (light gray) to broad (black). Histograms show the number of points that are included in each category of Proportional Habitable Area (PHA); columns are divided in four categories based on the percentage of occupation by the species (PPA/PHA)

Figure 3. Interpolated maps from Proportional Patch Area (PPA) values using Inverse Distance Weighted (IDW) method for the seasonality analysis without (left) and with (right) the inclusion of barriers (rivers); gray tones correspond to the size of the areas produced at each seed point from narrow (light gray) to broad (black). Histograms show the number of points that are included in each category of Proportional Habitable Area (PHA); columns are divided in four categories based on the percentage of occupation by the species (PPA/PHA)

CHAPTER 2

The effect of climate history and environmental granularity on species'
distributions in Africa and South America

ABSTRACT

Pleistocene refugia have been hypothesized based on current distributions of
species, associations with environments, phylogenetic relationships, and the fossil
record. These refugia are areas in which species could find suitable conditions
during the drier/colder conditions in the globally cool periods. Here, I explore the
effect of Last Glacial Maximum (LGM) cool conditions on environmentally and
geographically cohesive areas (mimicking species' distributions) chosen during the
last interglacial (LIG) period, using four levels of environmental restriction (5%, 10%,
15%, and 20% of overall variation). Reduction, expansion, displacement, and
disappearance of these areas were examined at each time step (LIG, LGM,
Present). Highly environmentally conserved areas matched proposed refugia in
South America, and Pleistocene climate changes seem to have had more extreme
effects on African environments than on South American environments. Impact of
climatic oscillations on environments was dependent on geographic location and the
level of ecological restriction: less-restricted environments showed expansions, while
tropical environments showed reductions or disappearance. Recent environmental
history affected species to different degrees depending on ecological niche
characteristics, which should be taken into account in phylogeographic studies;

biodiversity patterns depend critically on historical patterns of environmental granularity and its stability through time.

INTRODUCTION

Species' geographic distributions are determined by the location of environmentally suitable conditions on Earth, physiological and dispersal restrictions, interactions with other species, and phylogenetic history, among other factors (Brown et al. 1996; Elton 1927; Grinnell 1917; Hutchinson 1957; 1978; Janzen 1967; MacArthur 1972; MacArthur 1984; Whittaker et al. 1973). Although the degree to which each factor is involved in shaping the geographic range varies from species to species and region to region, all contribute to shaping processes, and thereby present-day biodiversity patterns (Haffer 1969; 1982; 1997; Mayr and O'Hara 1986).

Comparisons of biotas between Africa and South America indicate that several groups (e.g., birds, plants and amphibians) are more diverse in South America than in Africa (Colinvaux 1993; Duellman 1993; Fjeldså 1994; Goldblatt 1993). These two continents both hold a variety of environments, biomes, and ecosystems; however, they differ in terms of numbers of species that occur there. While South America holds >3200 bird species, >1300 anuran species, and >85,000 plant species, Africa has only about 2300 bird species, >600 anuran species, and around 45,000 plant species, in an area 1.8-fold larger than that of South America (Duellman 1993; Groombridge and Jenkins 2002).

The processes that have been considered as drivers for the creation of biodiversity are summarized by Haffer (1997; 2008), including geological, hydrological, ecological, and climatic phenomena that have shaped environmental conditions on the continents, promoting speciation.

Haffer (1969; 1982) proposed that the repeated climatic fluctuations during the Pleistocene changed distributions of the main vegetation types. These changes were manifested as cyclic reductions and expansions of their geographic distributions owing to the prevailing conditions (i.e., drier or wetter, colder or warmer). More importantly, the reductions were postulated to have fragmented habitat distributions as well, creating opportunities for speciation in the isolated fragments termed *refugia* (Vanzolini 1973; Vanzolini and Williams 1970). Vanzolini (1973) and Fjeldså (1994), further proposed that differences in refuge geometry between South America and Africa might explain the dramatic differences in their respective biodiversity richness.

Since its postulation, this Pleistocene refugium theory has been the subject of debate, with growing bodies of evidence both in support and in opposition (Bush 1994; Colinvaux et al. 1996; Colinvaux et al. 2000; Knapp and Mallet 2009; Mayr and O'Hara 1986; Moritz et al. 2000; Nichol 1999). Those in opposition either argue in favor of alternative ideas (Capparella 1991; 1997; Haffer 2008; Sick 1967) or argue against the absolute nature of the fragmentation presumably caused by savannah intrusion (Colinvaux 1993; Endler 1982). In spite of the controversy, however, refugium-based ideas are still used to explain diversification and phylogeographic patterns of flora and fauna (Avise et al. 1998; Pennington et al. 2004).

In a recent study, Rangel *et al.* (2007) reproduced observed patterns of avian diversity in South America based only on environmental conditions and their modification through a sine function emulating patterns of climatic variation. The simulation included basic rules for speciation, extinction, and invasion of new suitable areas at each time step. Their work has shown that, based on environmental characteristics and simple evolutionary rules, it is possible to replicate biodiversity patterns in South America; however, they did not explore effects of the changing climate on species' distributions (i.e., contractions, expansions) across the continent, nor have they assessed differential effects among continents.

Here, I explore the role of environmental heterogeneity in the production of species' distributional patterns at different levels of landscape granularity in South America and Africa during the last interglacial (LIG; 135,000 years ago) and last glacial maximum periods (LGM; 21,000 years ago). By means of simple transition rules between time periods I create a spatially explicit model assessing the main predictions of the Pleistocene refugium theory: (a) areas should exist in which climate conditions remained relatively constant through glacial and interglacial periods; (b) glacial maxima had major influences on the present distributions of species; and (c) differences in species richness and biodiversity patterns between Africa and South America are associated with differences in their spatiotemporal environmental characteristics.

METHODS

The goal of this study was to create suites of artificial species for which ecological niches were effectively held constant, but that could be tracked through time to see how climate fluctuations translate into biological diversity across South America and Africa. As such, the limits of the two study regions are the extents of the two continents.

Environmental data: I used seven climatic variables (annual mean temperature, mean diurnal range, maximum temperature of the warmest month, minimum temperature of coldest month, annual precipitation, precipitation of the wettest month and precipitation of the driest month) from the WorldClim dataset (Hijmans et al. 2005) to summarize present-day climatic conditions at a spatial resolution of 4 km. Past environmental conditions were drawn from a general circulation model (GCM) simulations based on the Community Climate System Model (CCSM, Collins et al. 2006) for two points in the past: LGM and LIG. The original LGM GCM data were downloaded from the PMIP2 website (http://www.pmip2.cnrs-gif.fr), with a spatial resolution of roughly 300 x 300 km, but were downscaled to a higher resolution (4 x 4 km) by calculating a difference map and smoothing the differences, as described in previous publications (Peterson and Nyári 2008; Waltari et al. 2007). A dataset representing LIG conditions based on the CCSM model (Collins et al. 2006), kindly provided by C. Amman, was downscaled to a spatial resolution of 4 km using the same methodology as described above by R. Hijmans (unpub. data). All three seven-variable datasets were standardized to permit comparisons between variables and allow tracking of identical values across datasets, using the following the formula:

$$z_{ijk} = \frac{x_{ijk} - \bar{x}_{.j1}}{s_{.j1}},$$

where z_{ijk} is the standardized value for the pixel i of the variable j and dataset k and;

j = {1,2,3,4,5,6,7} and k = {1 for LIG, 2 for LGM, 3 for Present}.

Environmental granularity: One thousand points representing the variety of environments were randomly selected across each continent independently. The corresponding values for the seven variables in the LIG database were assigned to each seed point. Euclidean distances were calculated from each seed point to all pixels in the map, using the formula:

$$d_{io} = \sqrt{\sum_{j=1}^{7}\left(x_{ij} - x_{oj}\right)^2} \, ,$$

where d_{io} is the Euclidean distance for pixel i to the seed point o and j indicates the seven environmental variables from the dataset. Once Euclidean distances were obtained, the environmentally closest pixels were selected at four thresholds (5%, 10%, 15%, and 20%) to create environmentally cohesive units akin to species' niche requirements; this task was achieved by finding the distance value at which 5%, 10%, 15%, or 20% of the distribution of values is included in the selection. Finally, I identified the subsets of the environmentally similar pixels that were connected spatially to the seed point, as a simulation of geographic distributions of artificial species at four levels of environmental specificity or ecological niche breadth (thresholds). From this process, I obtained 1000 maps (one for each seed point) showing the distribution of each of the contiguous, environmentally cohesive patches for each threshold on each continent during LIG.

Projections across time: Euclidean distances were also calculated for the LGM and Present datasets, but based on the original values and threshold values for all seed

points (i.e., values obtained from the LIG dataset). I proceeded to select pixels within the four thresholds and associated distance values derived from the LIG dataset. Given changing climatic conditions, the spatial representation of these environmental conditions could be reduced, expanded, or absent in particular scenarios, depending on the threshold used and environmental variation across space and time. I conserved only patches in the LGM that were geographically connected to the original patches in the LIG (Figure 1), thus allowing dispersal into contiguous areas only. This process was repeated at all threshold values for both continents.

The same temporal transition rules were applied to the LGM-Present step: only patches in the present geographically connected to patches in the LGM were preserved in the analysis. As such, this simulation is basically one of tracking an initial pool of 'species' distributed across the two continents, and filtering them by climate changes at two key points in time (LIG to LGM, LGM to present). Basic descriptive statistics (mean patch area, minimum and maximum patch area) were calculated to evaluate the effects of climate change through time.

Visualization: I plotted the seed points for which environments were represented in each dataset; only points for which environmental conditions were represented in each time step (given the similarity threshold and the connectivity restrictions explained above) are shown in Figure 2. The degree of overlap (O) between suitable areas from the two time steps was calculated as two ratios: O_{12}/A_1 and O_{12}/A_2, where O_{12} is the area of overlap between the suitable area in time 1 (A_1) and that in time 2 (A_2). The scatterplot contrasting these two ratios summarizes all possibilities of contraction, expansion, non-modification, and displacement of environment's

geographic location after each time step (Figure 2). Besides providing the overlap measures, this methodology made it possible to locate the overlapping areas spatially.

RESULTS

Environmental granularity

Using the most restrictive similarity threshold (5%), the 1000 seed points in South America produced patches that covered 93.83% of the continent, but only <5% of the continent was contained in >10% of these patches. These percentages increased rapidly as the threshold was broadened: environments represented by the patches covered >99% of the continent in all higher thresholds (10%, 15%, 20%), while areas occupied by the overlap of >10% of these patches were 75.41%, 96.09%, and 98.73%, respectively. In Africa, all corresponding percentages were smaller than those for South America, with areas represented of 81.23%, 97.12%, 99.33%, and 99.73% of the continent for the four thresholds respectively; areas of coincidence of >10% of the 'species' were 0%, 8.82%, 62.03% and 87.29% (Table 1).

LIG to LGM time step

In South America, the most restrictive threshold yielded maps of 844 seed points for which environmental conditions were present and contiguous between LIG and LGM. The areas represented for these patches were smaller in the LGM than in the LIG,

with average reductions of approximately 45%. For the 10% threshold, the proportion

of seed points represented in the LGM increased to 995 points; the average of their

areal extent decreased approximately 6%. The 15% and 20% thresholds retained all

1000 points and the average patch area increased still more. All paired t-tests

comparing patch sizes between these two time steps were highly significant ($P <$

0.01; Table 1).

In Africa, of the 1000 seed points at the most restrictive threshold, only 100 were

represented and contiguous in the LGM. As in South America, numbers of

environments found in the LGM increased with threshold breadth (Table 1). All four

thresholds showed decreased average area occupied by the selected environments

compared to South America. In general, LGM patches were smaller than LIG

patches, except for the highest threshold value, where LGM areas presented a small

increase (0.31%) in patch size, with highly significant paired t-tests ($P < 0.01$; Table

1).

The 5% threshold in South America created reductions of patch sizes around the

Amazon Basin (dark blue in Figure 3), while higher latitude areas and the Pacific

coastal regions showed high overlap between patches (dark red in Figure 3); a

mixture of expansions and displacements (light blue and light red in Figure 3)

separated these two regions. As the threshold was increased, the proportion of

points with high geographic overlap between time steps (dark red in Figure 3)

increased, becoming the dominant pattern for the continent. The pattern in Africa

was markedly different: while comparable and contiguous environments were not

found in the LGM for a great number of points, those that did persist presented small

overlap between time steps (light blue) or dramatic reductions of area (dark blue) for both GCMs. For higher threshold values, points in southern Africa and along the northern Atlantic coast increased in area, while most points elsewhere on the continent tended to show reduction of areas.

LGM to Present time step

In South America, most points for which environments were contiguous between LIG and LGM were also found in the present conditions: at the 5% threshold, only 20 of the 844 points from the LGM model were lost. At smaller thresholds, average patch size increased, while the broader thresholds yielded smaller patches in the present than in the LGM. In Africa, fewer LIG-LGM points were represented in present-day conditions (38, 45, 23 and, 36), suggesting a more dramatic climatic transition to present conditions than in South America (Table 1). However, the average size of areas under present conditions was larger in all cases than in the LGM conditions (Table 1).

The relationship between areas at LGM and present conditions for both continents is shown in Figure 3. In South America at LGM, stable areas (i.e., dark red points in Figure 3) were located towards the coasts (Caribbean coast of Colombia and Venezuela; Pacific coast of Ecuador, Peru, and Chile). The points at which environments were conserved during this time step dominated this continent at higher thresholds.

In Africa, points with more conserved areas (dark red in Figure 3) also increased as thresholds increased; however, they were less abundant than in South America, and were concentrated in the south and in northeast (Figure 3). For lower thresholds, environments associated with seed points tended to reduce in area (blue in Figure 3), while for higher thresholds, increasing areas were more abundant (red in Figure 3).

Environmental stability analysis

Figure 4 summarizes coincidence of overlapped areas (i.e., areas showing climate stability relative to niche limits) for all environments selected by the 1000 random points after the LIG-to-LGM and the LGM-to-Present time steps for both continents. Although scaling differed, patterns were similar across thresholds: the most environmentally stable areas occur along the eastern slope of the tropical Andes, northern coast of Venezuela, northern Colombia, southern Brazil, Uruguay, Paraguay and northern Argentina. In Africa, although coincidence was lower, the most stable areas were located in Nigeria, Benin, Togo, Ghana, and Ivory Coast, in the west, and Malawi, Zambia, Democratic Republic of Congo, Mozambique, and Zimbabwe, in the south.

DISCUSSION

This study offers one version of a null model of biological diversification. The scenario is one of many initial species with diverse distributions that pass through

two dramatic events of climate change. As species are not permitted to evolve ecologically, speciate, or disperse to disjunct suitable areas, the only process in this simulation is that of *loss* of species resulting from overly dramatic environmental change and spatial shifts in suitable areas over the past 135,000 years.

Expansions and contractions are both seen in the niche-based distributions of the artificial species in this study at each time step, owing to differential manifestation of climatic oscillations in different parts of the continents. As I increased the niche breadth of the species in the study, increases in area became more dominant in both time steps (LIG-to-LGM and LGM-to-Present); this phenomenon is expected because broader thresholds produce larger starting areas (LIG) that can in turn overlap more environmentally similar areas in the next time step (LGM) that would not be accessible to species with narrower niches. Some points along the Pacific coast in southern Chile showed reductions of the area in the LGM-to-Present time step, even at broad thresholds; this pattern was likely caused by non-climate-related reduction of coastal land areas owing to post-glacial sea level rise and associated marine intrusion.

Environmentally stable areas that I identified (Figure 5) yielded hypotheses of potential refugia that are roughly coincident with those proposed by Haffer (1969): Chocó, Nechí, Catatumbo, and East Peruvian refugia. Although using this methodology it was not possible to represent refuges proposed for the Amazon Basin (Imerí, Napo, Guiana, Madeira-Tapajós and Belém refuges; Figure 5), such areas have been reconstructed successfully in a previous version of this simulation that focused only on present-day climatic connectivity (Nakazawa, in review). These

results also coincide with results of previous studies based on retro-projections of ecological niches of present-day forest species (Bonaccorso et al. 2006; Peterson and Nyári 2008), and together indicate that Amazon forest ecosystems were indeed fragmented at LGM, at least in terms of the climatic parameters that frequently drive vegetation distributions.

Three areas of high stability were identified that do not coincide with the proposed refugia (Haffer 1969): (a) a small region on the northern coast of Venezuela (Figure 5j) which coincides with a refuge proposed by Vanzolini (Vanzolini 1973); (b) an area situated along the Venezuelan border with Guyana (Figure 5k) between the Imerí and Guiana refugia proposed by Haffer (1969); and (c) an extensive area of high coincidence in south-central Brazil, northeastern Argentina, and eastern Paraguay (Figure 5l) that includes a refuge proposed by Vanzolini (1973); highest coincidence within this area is shown east of Rio de Janeiro along the Atlantic coast of Brazil.

Artificial species' distributional areas showed notably smaller amounts of overlap among time periods in Africa than in South America (Figure 4). This result is related to two factors: (1) initial areas of African patches were considerably smaller than those in South America at the same thresholds (at least for the lower thresholds), and (2) the density of seed points for each continent was lower in Africa, owing to its larger area. In spite of differences in point density, a high proportion of the environments in both continents was sampled (Table 1) and, since overlapped areas between time steps depend only on their original location and the modified location owing to changing climate, the sampling density should not be a factor in interpretation of the patch overlap analysis. In South America, areas with highest

intertemporal coincidence correspond broadly to those areas proposed to have the highest number of relict lineages and "old" species in both continents (Fjeldså 1994), supporting the idea of the importance of environmentally stable areas through time.

In spite of the differences between continents, I found general patterns manifested on both continents: broader thresholds (i.e., generalist species) experienced broader habitable areas, and patch areas became bigger after each time step; specialist species (i.e., smaller thresholds) showed differential responses to climate change, with both increases and decreases in size between time periods. In real-world terms, specialist species are projected to see increment, reduction, displacement, or disappearance of their environmentally suitable areas, and thus may be more likely to go extinct; on the other hand, species with broader niches have better access to more suitable areas, allowing them to maintain broader areas of distribution in spite of changing environmental conditions. Besides niche breadth, speciation rates also play important roles in producing biodiversity patterns on continents. Although speciation was explicitly not included in my simulations, specialist species clearly experience more fragmentation, and may see more potential for speciation.

Differences between maps of overlap (Figure 4) suggest that South America presented more refugia than Africa through the last 135,000 years. Species with narrow niches (5% and 10%) in Africa tended simply to go extinct, while most species in South America were able to find suitable areas through time regardless of the niche breadth (Table 1). These results suggest that (a) climatic changes had more drastic impacts on artificial species in Africa than in South America; (b) owing to the intensity of these impacts, species could survive only by having broad niches

or following those favorable conditions over broader areas; and (c) high environmental heterogeneity in South America could have facilitated survival of species through LGM, as opposed to more homogeneous environmental conditions in Africa.

The present work assumed niche conservatism, no speciation, and limited dispersal, in contrast to other factors considered in recent studies in the same vein (Rangel et al. 2007). In spite of the relatively simple model, my work permitted analysis of effects of changing climates on patterns of distribution of artificially created species, and, more importantly, discrimination of effects resulting from differences in niche breadth and geographic location. While the goal of Rangel *et al.* (2007) was to reproduce observed species richness patterns in South America, I focused on the analysis of the effects that changing climates have on shaping species' distributions and, thus, biodiversity. Future studies should include dispersal factors that could allow species to detect and colonize disjunct patches of suitable habitats, perhaps incorporating speciation as an additional factor; inclusion of greater temporal detail would allow investigators to track the 'behavior' of the patches through a changing environment and test more carefully for area connectivity in the past (Costa 2003; Linder et al. 2000; Linder 2001; Pennington et al. 2004; Ron 2000).

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LITERATURE CITED

Avise, J. C., D. Walker, and G. C. Johns. 1998. Speciation durations and Pleistocene effects on vertebrate phylogeography. Proceedings of the Royal Society of London B 265:1707-1712.

Bonaccorso, E., I. Koch, and A. T. Peterson. 2006. Pleistocene fragmentation of Amazon species' ranges. Diversity and Distributions 12:157-164.

Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: Size, shape, boundaries, and internal structure. Annual Review of Ecology and Systematics 27:597-623.

Bush, M. B. 1994. Amazonian speciation: A necessarily complex model. Journal of Biogeography 21:5-17.

Capparella, A. 1991. Neotropical avian diversity and riverine barriers. Acta XX Congressus Internationalis Ornithologici 20:307-316.

Colinvaux, P. A. 1993. Pleistocene biogeography and diversity in tropical forests of South America *in* P. Goldblatt, ed. Biological Relationships between Africa and South America. New Haven, Yale University Press.

Colinvaux, P. A., P. E. De Oliveira, J. E. Moreno, M. C. Miller, and M. B. Bush. 1996. A long pollen record from lowland Amazonia: Forest and cooling in glacial times. Science 274:85-88.

Colinvaux, P. A., P. E. De Olivera, and M. B. Bush. 2000. Amazonian and

    Neotropical plant communities on glacial time-scales: The failure of the aridity

    and refuge hypothesis. Quaternary Science Reviews 19:141-169.

Collins, W. D., C. M. Bitz, M. L. Blackmon, G. B. Bonan, C. S. Bretherton, J. A.

    Carton, P. Chang, S. C. Doney, J. J. Hack, T. B. Henderson, J. T. Kiehl, W.

    G. Large, D. S. McKenna, B. D. Santer, and R. D. Smith. 2006. The

    Community Climate System Model version 3 (CCSM3). Journal of Climate

    19:2122-2143.

Costa, L. P. 2003. The historical bridge between the Amazon and the Atlantic Forest

    of Brazil: A study of molecular phylogeography with small mammals. Journal

    of Biogeography 30:71-86.

Duellman, W. E. 1993. Anphibians in Africa and South America: Evolutionary history

    and ecological comparisons *in* P. Goldblatt, ed. Biological Relationships

    between Africa and South America. New Haven, Yale University Press.

Elton, C. 1927. Animal Ecology. London, Sidgwick and Jackson.

Endler, J. 1982. Pleistocene forest refuges: Fact or fancy?, Pages 179-200 *in* G. T.

    Prance, ed. Biological Diversification in the Tropics. New York, Columbia

    University Press.

Fjeldså, J. 1994. Geographical patterns for relict and young species of birds in Africa

    and South America and implications for conservation priorities. Biodiversity

    and Conservation 3:207-226.

Goldblatt, P. 1993. Biological Relationships between Africa and South America. New

    Haven, Yale University Press.

Grinnell, J. 1917. The niche-relationships of the California thrasher. Auk 34:427-433.

Groombridge, B., and M. D. Jenkins. 2002. World Atlas of Biodiversity. Berkeley, California, University of California Press.

Haffer, J. 1969. Speciation in Amazonian forest birds. Science 195:131-137.

—. 1982. General aspects of the refuge theory, Pages 6–24. *in* G. T. Prance, ed. Biological Diversification in the Tropics. New York, Columbia University Press.

—. 1997. Alternative models of vertebrate speciation in Amazonia: An overview. Biodiversity and Conservation 6:451-476.

—. 2008. Hypotheses to explain the orign of species in Amazonia. Brazilian Journal of Biology 68:917-947.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965-1978.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415-427.

—. 1978. An Introduction to Population Ecology. New Haven, Connecticut, Yale University Press.

Janzen, D. H. 1967. Why mountain passes are higher in the Tropics. American Naturalist 101:233-249.

Knapp, S., and J. Mallet. 2009. Refuting refugia? Ecology 400:71-71.

Linder, E. T., M.-A. Villard, B. A. Maurer, and E. V. Schmidt. 2000. Geographic range structure in North American landbirds: Variation with migratory strategy, trophic level and breeding habitat. Ecography 23:678-686.

Linder, H. P. 2001. Diversity and endemism in sub-Saharan tropical Africa. Journal of
Biogeography 28:169-182.

MacArthur, R. H. 1972. Geographical Ecology. New York, Harper & Row Publishers.

—. 1984. Geographical Ecology: Patterns in the Distribution of Species. New York,
Harper & Row Publishers.

Mayr, E., and R. J. O'Hara. 1986. The biogeographic evidence supporting the
Pleistocene forest refuge hypothesis. Evolution 40:55-67.

Moritz, C., J. L. Patton, C. J. Schneider, and T. B. Smith. 2000. Diversification of
rainforest faunas: An integrated molecular approach. Annual Review of
Ecology and Systematics 31:533-563.

Nichol, J. E. 1999. Geomorphological evidence and Pleistocene refugia in Africa.
Geographical Journal 165:79-89.

Pennington, R. T., M. Lavin, D. E. Prado, C. A. Pendry, S. K. Peli, and C. A.
Butterworth. 2004. Historical climate change and speciation: Neotropical
seasonally dry forest plants show patterns of both Tertiary and Quaternary
diversification. Philosophical Transactions of the Royal Society of London B
359:515-537.

Peterson, A. T., and Á. S. Nyári. 2008. Ecological niche conservatism and
Pleistocene refugia in the Thrush-like Mourner, *Schiffornis* sp., in the
Neotropics. Evolution 62:173-183.

Rangel, T. F. L. V. B., J. A. F. Diniz-Filho, and R. K. Colwell. 2007. Species richness
and evolutionary niche dynamics: A spatial pattern-oriented simulation
experiment. American Naturalist 170:602-616.

Ron, S. R. 2000. Biogeographic area relationships of lowland Neotropical rainforest based on raw distributions of vertebrate groups. Biological Journal of the Linnean Society 71:379-402.

Sick, H. 1967. Rios e enchentes na Amazônia como obstáculo para a avifauna. Atas do Simpósio sôbre a Biota Amaônica 5(Zoologia):495-520.

Vanzolini, P. E. 1973. Paleoclimates, relief, and species multiplication in equatorial forests *in* B. J. Meggers, E. S. Ayensi, and W. S. Duckworth, eds. Tropical Forest Ecosystems in Africa and South America: A Comprehensive Review. Washington, D.C., Smithsonian Institution Press.

Vanzolini, P. E., and E. E. Williams. 1970. South American anoles: The geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). Arquivos de Zoologia (São Paulo) 19:1-298.

Waltari, E., R. J. Hijmans, A. T. Peterson, Á. S. Nyári, S. L. Perkins, and R. Guralnick. 2007. Locating Pleistocene refugia: Comparing phylogeographic and ecological niche model predictions. PLoS ONE 2:e563.

Whittaker, R. H., S. A. Levin, and R. B. Root. 1973. Niche, habitat, and ecotope. American Naturalist 107:321-338.

Table 1: Area occupied by distributions of virtual species on both continents considering four niche-breadth thresholds applied to the LIG dataset; mean area across all extant patches is presented as percentage of the total area in the continent. For LGM, number of points for which environmentally similar patches matching connectivity restrictions with LIG patches is presented; number of points lost from one time step to the next is in parentheses. Difference in patch area compares LIG to LGM and LGM to Present. ** indicates highly significant (*P* < 0.01) in paired *t*-tests.

	Threshold value	South America				Africa			
		5%	10%	15%	20%	5%	10%	15%	20%
LIG	Total area in patches (%)	93.82	99.22	99.51	99.6	81.23	97.12	99.33	99.73
	Area covered by >10% of patches (%)	4.77	75.41	96.09	98.73	0	8.82	62.03	87.29
LGM	Mean area (% of total)	3.66	23.41	51.8	72.43	0.64	4.002	13.53	29.23
	# points	844 (156)	995 (5)	1000 (0)	1000 (0)	100 (900)	556 (444)	839 (161)	973 (27)
	Difference in patch area from prev. time step (%)	-45.53**	-6.06**	1.62**	4.23**	-97.24**	-88.19**	-71.16**	-42.88***
Present	# points	824 (20)	994 (1)	1000 (0)	1000 (0)	62 (38)	511 (45)	816 (23)	964 (36)
	Difference in patch area from prev. time step (%)	67.69**	10.52**	-1.87**	-4.93**	813.84	222.17**	71.57**	14.28**

1) LIG: selection of pixels environmentally similar (light blue) to the seed point (red star) based on a particular threshold. Only pixels connected spatially to the seed point are retained (dark blue).

2) LGM: selection of LGM environmentally similar pixels based on LIG conditions at the seed point (light blue); but only those connected spatially to LIG distributions (gray) were retained as LGM distributions (dark blue).

3) Present: selection of present-day environmentally similar pixels based on LIG conditions at the seed point (light blue); but only those connected to LGM distributions (gray) were retained as present distributions (dark blue).

Figure 1. Methodology followed for patch selection at each time step from areas environmentally similar to the seed point, and geographic overlap with previous location. Overlap between time steps was calculated as the intersection of the two areas of distribution.
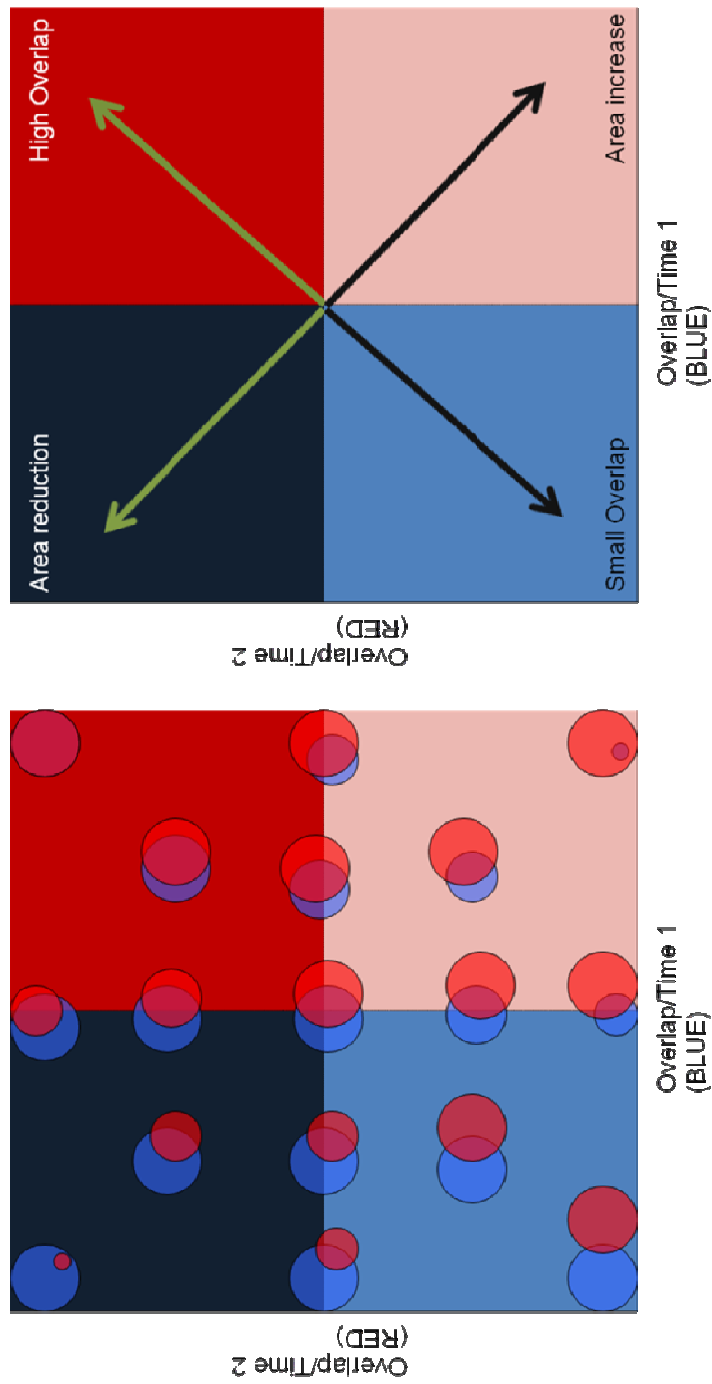
Figure 2. Relationship of the two ratios O/A_1 (x axis) and O/A_2 (y axis): circles represent areas in

time 1 (blue) and time 2 (red). Points falling in blue quadrants experienced reduction of area

from time 1 to 2, while red quadrants experienced increases in area. Background colors (light

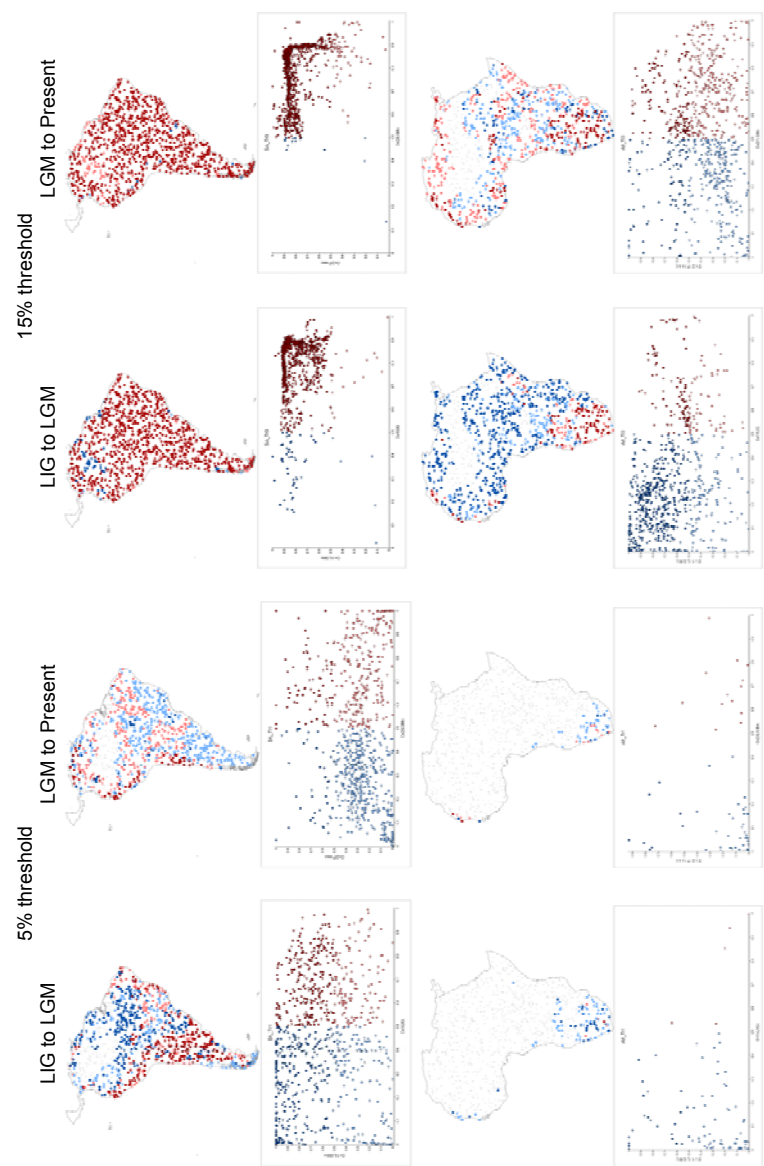blue, light red, dark blue, and dark red) are used in Figures 3 and 4.

Figure 3. Seed points colored according to the level of overlap between the two time steps and the reduction or expansion of areas from one time to the next based on the CCSM model; colors correspond to Figure 2.
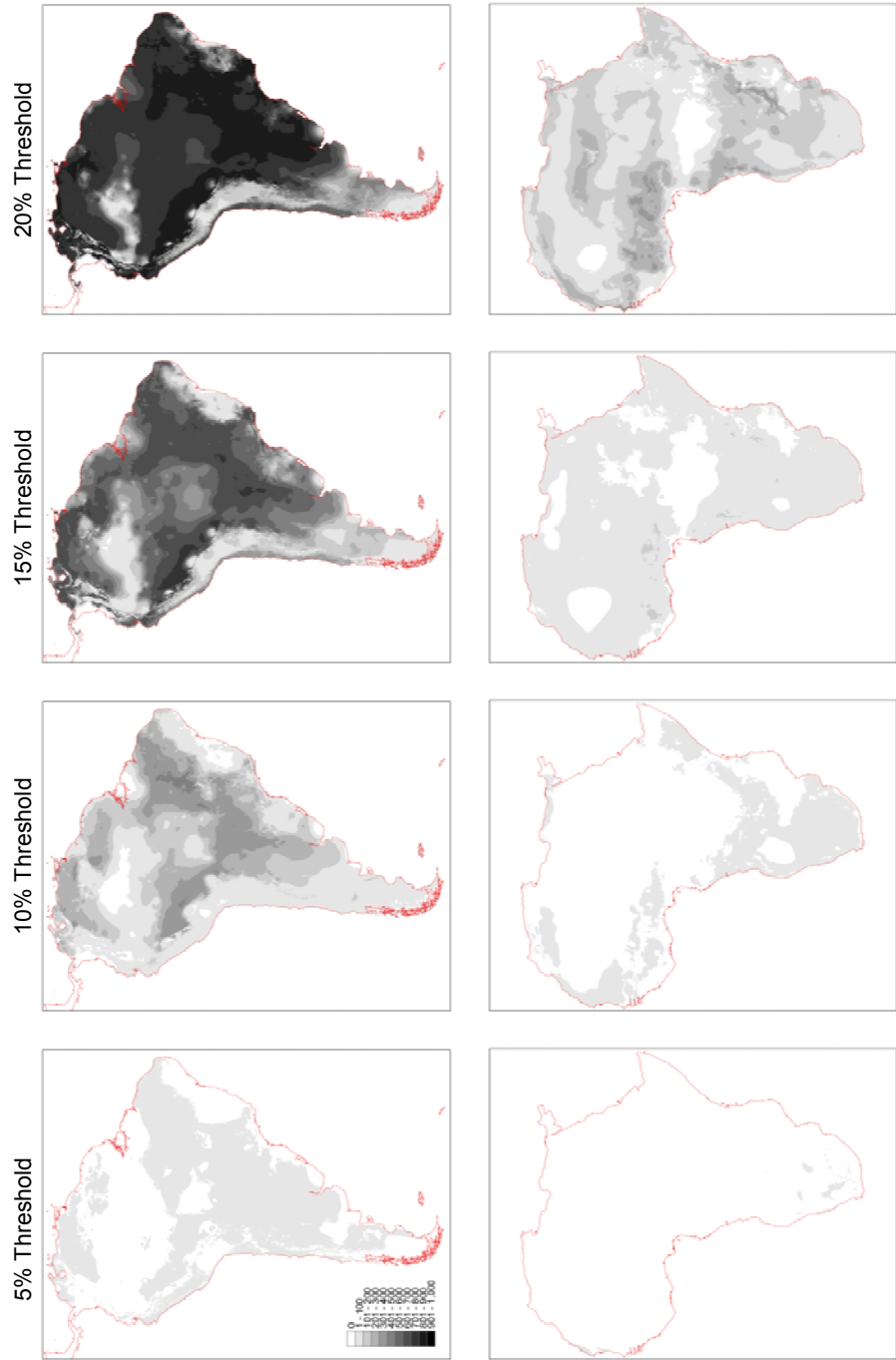
Figure 4. Coincidence of areas overlapping between LGM and present-day distributions of virtual species. Darker areas represent higher coincidence of overlapped areas, and thus more environmentally stable areas, at each threshold.

Figure 5. Coincidence of overlapping areas for the LGM-Present time step using species with the broadest niches (95% of the total in dark gray; 90% in light gray). Refugia proposed by Haffer (stippled areas): (a) Chocó, (b) Catatumbo, (c) East Peruvian, (d) Nechí, (e) Napo, (f) Imerí, (g) Madeira-Tapajós, (h) Guiana, and (i) Belém; refugia proposed by Vanzolini (hatched areas); and other areas of high environmental stability (j, k and l).

CHAPTER 3

Seasonality, rivers, climatic history, and niche breadth as factors shaping

biological diversity patterns in South America

ABSTRACT

The study of biodiversity has lead to the development of a variety of hypotheses for

explaining patterns observed in nature; the dominant hypothesis are climatic and

topographic heterogeneity, latitudinal gradients, associations with system energy,

and structure by biogeographic history, among others. Researchers have

accumulated evidence supporting each of these hypotheses, but in large part without

achieving any consensus. In the present study, I examine the role of four factors

(present-day climate conditions, biogeographic barriers, seasonality, and climate

history) in shaping the distributional characteristics of artificial biotas created from

species with similar niche breadths (at three niche breadth levels). These simulations

were compared to one another and to reported bird distributional summaries from

NatureServe in terms of range-diversity plots. Bird distributions obtained as

generalized polygons failed to reproduce those areas characterized by very

distinctive sets of species; consequently, precautions should be taken when using

them in macroecological studies, especially in studies requiring high spatial detail, as

in conservation efforts. Factors shaping biodiversity on Earth are many, and the

interactions between these factors are mostly unknown; this analysis shows how

biodiversity patterns are affected by single factors, and analyzes such effects from

the point of view of both species and sites; covariance maps also helped

understanding these processes spatially.

INTRODUCTION

Several hypotheses have been proposed to explain observed patterns of terrestrial

biodiversity (i.e., the number of species at a particular site), including exploring

relationships between biodiversity parameters and environmental productivity and/or

energy (Francis and Currie 1998; Francis and Currie 2003; Hutchinson 1959;

MacArthur 1984), climatic events through Earth history (Currie 1991; Haffer 1969;

Ricklefs 2004; Ricklefs et al. 1999), latitudinal gradients (Gaston 2000; Pianka 1966),

landscape heterogeneity (Forman 1995; Huston 1994; Rosenzweig 1995), and

environmental homogeneity (Janzen 1967; Klopfer 1959), among other factors.

These hypotheses can be divided into environment-based and history-based

explanations of biodiversity origin; debates between these two fundamental ideas

have improved the understanding of the processes that generate biodiversity

(Francis and Currie 1998; Francis and Currie 2003; Ricklefs 2004; Ricklefs et al.

1999). In spite of all this controversy, the extent to which these factors shape

distributions of species is not clear; it is likely that a combination of environmental

and historic processes is involved in the creation of biodiversity patterns (Ricklefs

2004; Wiens and Donoghue 2004).

Whittaker (1972) recognized three measures of biodiversity: (a) the number of

species found at a particular site within a region, or α-diversity; (b) the regional

species' richness, or γ-diversity; and (c) the proportional richness of a site compared

to the total richness of the region to which it belongs or β-diversity. Although the concept of β-diversity has been redefined and means for its calculation have been proposed by several authors (see Koleff et al. 2003), Whittaker's (1972) β-diversity remains an easily interpretable measure that can be derived from a presence-absence matrix (PAM), and has direct relation to α- and γ-diversity measures (Arita et al. 2008; Koleff et al. 2003; Whittaker 1972).

PAMs are commonly used in macroecology and biogeography to summarize distributional areas of species (Brown et al. 1996; Gaston 2003) and numbers of species at sites (Rosenzweig 1995). A PAM describes the distribution of *S* species in *N* sites; its elements $\delta_{ij}(i,j)$ indicate presence (1) or absence (0) of species *i* at site *j* (Gotelli 2000).

Diversity of site *j* (s_j) is the sum of presences in column *j* and represents the number of species occurring at that particular site (α-diversity), while the range of species *i* (n_i) is the number of sites in which the species is found, calculated as the sum of presences in each row (Arita et al. 2008):

$$s_j = \sum_{i=1}^{S} \delta(i,j) \quad \text{and} \quad n_i = \sum_{j=1}^{N} \delta(i,j)$$

By dividing s_j by *S* and n_i by *N*, we obtain the species diversity in each site as a proportion of the total number of species in the region ($s_j{}^*$), and the range size of all species as a proportion of the total number of sites in the region ($n_i{}^*$):

$$s^*{}_j = \frac{1}{S} s_j \quad \text{and} \quad n^*{}_i = \frac{1}{N} n_i$$

Averages of diversity ($\bar{s}$), proportional diversity ($\bar{s}^*$), ranges ($\bar{n}$), and proportional ranges ($\bar{n}^*$) are given by:

$$\bar{s} = \frac{1}{N} \sum_{j=1}^{N} s_j$$

$$\bar{n} = \frac{1}{S} \sum_{i=1}^{S} n_i$$

$$\bar{s}^* = \frac{1}{S} \bar{s}$$

$$\bar{n}^* = \frac{1}{N} \bar{n}$$

Interestingly, these last two equations can be equated to each other so the average of the proportional diversities is equal to the average of the proportional ranges:

$$\bar{s}^* = \frac{1}{N} \sum_{j=1}^{N} s^*_j = \frac{1}{N} \sum_{j=1}^{N} \frac{1}{S} \sum_{i=1}^{S} \delta(i,j) = \frac{1}{S} \sum_{i=1}^{S} \frac{1}{N} \sum_{j=1}^{N} \delta(i,j) = \frac{1}{S} \sum_{i=1}^{S} n_i^* = \bar{n}^*$$

The total number of all species occurrences is called the fill of the matrix ($f = \sum_{j=1}^{N} s_j = \sum_{i=1}^{S} n_i$). Its proportional value is $f^* = f/NS$ relative to the dimension of the PAM, we then have (Arita et al. 2008):

$$f^* = \frac{1}{NS} f$$

$$f^* = \frac{1}{NS} \sum_{j=1}^{N} s_j = \frac{1}{NS} \sum_{i=1}^{S} n_i$$

$$f^* = \frac{1}{NS}\sum_{j=1}^{N}\sum_{i=1}^{S}\delta(i,j) = \frac{1}{NS}\sum_{i=1}^{S}\sum_{j=1}^{N}\delta(i,j)$$

$$f^* = \bar{s}^* = \bar{n}^*$$

Whittaker's {, 1972 #454} β-diversity is the ratio between the regional diversity and the average local diversity, which in our notation is:

$$\beta = \frac{S}{\bar{s}} = (\bar{s}^*)^{-1} \quad \text{or} \quad \beta = \frac{N}{\bar{n}} = (\bar{n}^*)^{-1}$$

$$\text{Thus, } \beta^{-1} = f^* = \bar{s}^* = \bar{n}^*$$

The average local diversity and the average range of species are entirely determined by the marginal values of the matrix; for this reason, identical values of alpha and beta diversities can be obtained from matrices with different structures, as long as the marginal values don't change.

Covariance between ranges of species or between sites' species composition are parameters that describe the structure of communities based on the PAM. The covariance of ranges between species i and l is given by:

$$\rho_n(i,l) = \frac{1}{N}\sum_{j=1}^{N}\delta(i,j)\delta(l,j) - \frac{n_i}{N}\frac{n_l}{N}$$

The second member of this equation is the proportion of sites where both species (i and l) co-occur minus the proportion of co-occurrences under a null hypothesis of no association. Generalizing this equation to calculate the average covariance of species i with all the other species we have:

$$\bar{\rho}_n(i) = \frac{1}{S} \sum_{l=1}^{S} \rho_n(i, l)$$

$$\bar{\rho}_n(i) = \frac{1}{S} \sum_{l=1}^{S} \left(\frac{1}{N} \sum_{j=1}^{N} \delta(i,j)\delta(l,j) - \frac{n_i}{N}\frac{n_l}{N} \right)$$

$$\bar{\rho}_n(i) = \frac{1}{SN} \left(\sum_{j=1}^{N} \sum_{l=1}^{S} \delta(i,j)\delta(l,j) - \frac{n_i}{N} \sum_{l=1}^{S} n_l \right)$$

$$\bar{\rho}_n(i) = \frac{1}{SN} \left(\sum_{j=1}^{N} \delta(i,j) \sum_{l=1}^{S} \delta(l,j) - n_i{}^* \sum_{l=1}^{S} n_l \right)$$

$$\bar{\rho}_n(i) = \frac{1}{SN} \sum_{j=1}^{N} \delta(i,j)s_j - n_i{}^*\bar{n}^*$$

$$\bar{\rho}_n(i) = \frac{1}{N} \sum_{j=1}^{N} \delta(i,j)s_j{}^* - n_i{}^*\bar{n}^*$$

Since only diversity at sites where species i is present (n_i) are taken into account we have that N can be substituted by n_i, then the covariance becomes:

$$\bar{\rho}_n(i) = \frac{1}{n_i} \sum_{j=1}^{N} \delta(i,j)s_j{}^* - n_i{}^*\bar{n}^*$$

$$\bar{\rho}_n(i) = n_i{}^*(\bar{s}_j{}^* - \bar{n}^*)$$

$$n_i{}^* = \frac{\bar{\rho}_n(i)}{\bar{s}_j{}^* - \bar{s}^*}$$

In this equation, the proportional range of species *i* is related to the proportional richness associated to it, in other words, it tells us whether a species is associated with very diverse spots, or rather very impoverished ones. The same argument can be constructed for the covariance between sites yielding the calculation of the average (with respect to the richness of the site) of the proportional ranges of all species present at site *j*:

$$s_j^* = \frac{\bar{\rho}_n(j)}{\bar{n}_j^* - \bar{n}^*}$$

The last two equations relate to the concepts of associated richness for a species and the associated ranges for a site, respectively (Arita et al. 2008). They are powerful tools for analyzing the PAM and describe the association between species and between sites through the covariance.

Recently, computational models have been built using digital environmental datasets and a variety of analytical tools to analyze and replicate the biodiversity patterns of diverse groups of organisms (Rahbek et al. 2007; Rangel et al. 2007). Environmental differences from one site to neighboring sites have been correlated to β-diversity at the focal site, showing that environmental heterogeneity and climate conditions can explain variations in diversity among regions independently of species richness (Melo et al. 2009). In spite of these efforts, it is still not clear how factors from the environment- and history-based explanations interact to produce the observed patterns of biodiversity on the continents (McKnight et al. 2007).

In previous studies, I created sets of artificial species where niche breadths were defined in a multivariate environmental space, and their distributions were based on

their environmental characteristics and their spatial location. Using these species, I explored the effect that biogeographic barriers and environment variations through the year have on species range sizes with different niche breadths (Nakazawa Submitted-a); and species' response to climatic oscillations in the last 135,000 years ago by tracking their extinction, range expansion, range displacement, and range reduction (Nakazawa Submitted-b).

Here, I use the framework of Arita *et al.* (2008) to compare the structure of artificial biotas produced by analysis of environmental granularity across South America. In particular, I simulate biotas under different scenarios: (a) environmental granularity only, (b) environmental granularity and riverine barriers, (c) environmental granularity considering seasonality, (d) environmental granularity considering seasonality and riverine barriers, and (e) environmental granularity in view of the last 135,000 years of climatic history. I use range-diversity plots to summarize the biodiversity pattern in each of the artificial biotas created under each scenario. I explore effects of seasonality, climatic history, and riverine barriers on the structure of artificial biotas across the continent, and compare them to similar plots derived from distributional summaries for real faunas.

METHODS

Environmental data: I selected 1000 random points across South America representing the environmental diversity of the continent as seed points for generation of artificial species. These points were matched with environmental layers of present-day conditions from the WorldClim dataset (Hijmans et al. 2005); and

interpolated datasets from the Community Climate System Model version 3 (CCSM3, Collins et al. 2006) for environmental conditions in the last interglacial period (LIG: 135,000 years ago) and last glacial maximum (LGM: 21,000 years ago). Original CCSM3 data were obtained from the PMIP2 website (http://www.pmip2.cnrs-gif.fr) at a spatial resolution of roughly 300 x 300 km; this dataset was used to calculate differences between past and present climate conditions. Using a spline function, these differences were interpolated to a 2.5' spatial resolution and added to the WorldClim dataset to calculate past environmental conditions (Peterson and Nyári 2008; Waltari et al. 2007). All layers were resampled to a spatial resolution of 4 x 4 km using the Albers Equal Area projection for South America. Three environmental datasets were built as follows:

PRES: Present day dataset: annual mean temperature, mean diurnal range, maximum temperature of the warmest month, minimum temperature of coldest month, annual precipitation, precipitation of the wettest month and precipitation of the driest month.

SEAS: Seasonal dataset: included mean of temperature value, maximum temperature, minimum temperature and precipitation in each of the following months: January, April, July and October.

HIST: Historic datasets: the same variables used for the PRES dataset were considered for two historic datasets: one representing the environmental conditions in the last interglacial period (HIST-LIG) and a second for the last glacial maximum (HIST-LGM).

Environmental granularity levels: Each of the 1000 seed points were intersected with the data layers of each of the datasets described above to retrieve the environmental conditions at those sites. For each point, the Euclidean distance in multivariate environmental space was then calculated to all other pixels using all variables in the dataset. These distance values were treated as a measure of environmental similarity to that particular seed point, and three thresholds were applied to select pixels with the highest similarity (i.e., the most similar 5%, 10%, and 20% of the range of values). These threshold values can be thought of as niche breadth levels (from narrow to broad).

The distribution of the artificial species was then created by identifying all pixels included within the similarity threshold that were spatially contiguous to the seed point. This procedure assured the creation of spatially and environmentally cohesive units that could be represented on a map. Artificial species created with the same threshold value across all seed points thus constituted an artificial biota with species of similar niche breadth randomly distributed across the continent.

The first two scenarios were built with artificial species created using the PRES and SEAS datasets: (a) present day conditions only (P), (b) present day conditions with seasonality (S). I included the presence of rivers known to constitute barriers for distributions of birds in South America as an additional limiting factor for distributions of species in each of these two datasets, yielding two more scenarios: (c) present-day conditions with rivers (PR) and (d) present-day conditions with both seasonality and rivers (SR).

The fifth scenario was built via the creation of artificial species in a similar fashion,
but using environmental conditions of HIST-LIG. Species' ranges were tracked
through time assuming niche conservatism in two time steps: (a) HIST-LIG to HIST-
LGM, and (b) HIST-LGM to PRES. At each time step transition, species were
eliminated if suitable areas were not found, or if suitable areas were not connected
spatially to the distributional area in the previous time step. The resulting distributions
under present-day conditions constitute the final scenario: (e) present-day conditions
incorporating climatic history (H).

Bird distributional data: To provide real-life comparison with biodiversity patterns in a
faunal group, I obtained distributional maps from the NatureServe webpage
(http://www.natureserve.org/) for all bird species of the Western Hemisphere (Ridgely
et al. 2007). From this dataset, 2639 species were selected because their
geographic ranges were completely or partially included in the study area; this real-
world example is referred as scenario B, although we note at the outset serious
concerns regarding the level of generalization of species ranges' representation (Jetz
et al. 2008).

Range-diversity plots: Although artificial species distributions were produced at a
high spatial resolution (4 km pixels), the level of generalization of the bird distribution
data does not permit analysis at that resolution; therefore, PAMs were built for each
of the six scenarios (P, PR, S, SR, H, and B) using a sampling grid of 1925 squares
of 100 x 100 km, at each similarity threshold independently (note that no threshold

considerations are available for B) and analyzed by species and by sites. Range-diversity plots were constructed by plotting the mean proportional species diversity ($\bar{s}_i{}^*$) against the proportional range size (n_i) in the analysis by sites; and the mean proportional range size ($\bar{n}_j{}^*$) to the proportional species diversity (s_j) in the analysis by species (Figure 1). The proportional fill of the matrix (f^* or $1/\beta$) is the same in both plots representing the line of zero covariance and determining the general area where the cloud of points falls (Figure 1A). Points are also restricted to the area between maximum and minimum covariance; areas outside of these limits are not available owing to mathematic restrictions inherent to the PAM (Arita et al. 2008).

Histograms of covariance values from both configurations of the PAM were produced for all scenarios and compared to each other via quantile-quantile plots (Q-Q plots) for each similarity threshold. I also linked the covariance values of the analysis by site to the original 100 x 100 km squares for visual analysis of the geographic distribution of covariance values under each scenario. All calculations and manipulations were performed in R version 2.4.1 and all map displays were developed in ArcMap 9.3.

RESULTS

Analysis by site: The PAMs extracted from sets of artificial species created in the P scenario showed smaller β-diversity values when broader niches were used (Figure 2), producing a shift to the right of f^* in the range-diversity plots (Figures 3 and 4). Minimum covariance was negative and maximum covariance positive in all cases; as

broader niches were used, covariance increased in absolute values (Table 1). Sites with higher values of both variables used to built the range-diversity plots (s_j and $\bar{n}_j{}^*$) are also evident in species of broader niches (Figures 3 and 4).

When rivers were included (PR scenario), all of the tendencies identified in the P scenario (i.e., smaller minimum covariances, greater maximum covariances, lower β-diversity, and higher s_j and $\bar{n}_j{}^*$ values) were also found for species with broader versus narrower niche. However, the magnitude of these changes was smaller in the scenario PR than in P (Figure 2 and Table 1).

In the same way, scenarios S and SR presented similar tendencies and contrasts as described for scenarios P and PR. However, f^*, s_j and $\bar{n}_j{}^*$ values were higher in scenarios including seasonality (S and SR) than scenarios without seasonality (P and PR) at the corresponding niche breadth values, yielding, interestingly, low values of β-diversity at all similarity thresholds (Figure 2). Maximum and minimum covariances in scenarios S and SR were reduced in absolute values with broader niches; however, absolute covariance values from SR were always higher than those in S (Table 1).

Scenario H also presented reduction of β-diversity as similarity threshold increased; however, β-diversity values were always higher than those in S and SR scenarios and lower than those in P and PR scenarios (Figure 2). The range-diversity plot for the birds of South America (B) shows positive minimum covariance (Figure 1 and Table 1), as contrasted with the rest of the scenarios, which had negative minimum covariances. QQ-plots comparing covariance histograms obtained from the analysis by sites (with 20% threshold) are shown in Figure 5: the thin line represents identity

of the covariance histograms between the two scenarios compared; all covariance distributions are different from each other.

Covariance maps (Figure 6) show drastic changes in spatial distribution of highest and lowest covariance values between scenarios. The highest covariances in the P scenario are found around the Amazon Basin, and the lowest covariances are found in the Andes; when rivers are included (PR), sites with highest covariance shift to the south of the Amazon Basin. More drastic changes are appreciable when comparing maps for S and SR, where high covariance values switch from southern Argentina and the Pacific coast to central Brazil when rivers are included (Figure 6). The covariance spatial distribution for scenario H was broadly coincident with that shown in scenario P.

Analysis by species: As explained above, f^* is the same in both types of range-diversity plots; therefore, its behavior is the same as in the previous section. Mean proportional species diversity $\bar{s}_i^*$ values are normally higher for scenarios S and SR than for scenarios P and PR; the same pattern can be seen for proportional range-size values (n_i), with the highest values for scenario S. When comparing scenarios including rivers PR and SR to scenarios without rivers (P and S, respectively), reductions in f^*, n_i, and $\bar{s}_i^*$ are noticeable (Figure 4).

As broader niches were used, absolute values of covariances increased in scenarios P and PR, while smaller values were shown for S and SR scenarios. For scenario H, maximum covariance increased from the narrow to the intermediate niche breadth and then decreased at the broadest niche breadth. As opposed to the analysis by

site, the analysis of Neotropical birds (B) yielded a negative value for the minimum

covariance (Table 1) reflected in the two-tailed range-distribution plot for this

scenario (Figure 5). QQ-plots showed that the distributions of covariance derived

from the analysis by species were different for all scenarios.

DISCUSSION

Niche breadth: Broader niches reduce environmental limitations for species to

disperse and are, in general, translated into larger range sizes. The methodology I

used to create artificial species could be thought of as a way of measuring the spatial

"grain" of the landscape in terms of patches with similar environments as a function

of niche breadth, broader niches fragment that landscape into bigger patches. Given

that the study area is finite (i.e., South America), greater overlap between

distributional areas is expected as a result of the increase in niche breadth of the

artificial species. All scenarios showed increasing range overlap with increasing

niche breadth consistently, which is expected as explained by the mid-domain effect

(Colwell and Lees 2000; Colwell et al. 2004).

Similarly, bigger ranges create higher species richness on average, causing sites to

share more species with each other; as a consequence, positive covariance between

sites should increase. Table 1 shows this expected pattern in the analysis by sites,

but also, negative covariances become bigger in absolute value, indicating the

persistence of low-diversity sites in which species' ranges are small and the species

composition is different when comparing to all other sites in the region (Figure 6).

Rivers: Rivers represented an effective limiting factor for species' distributions that kept species from occupying suitable areas on the other side of the river; hence, smaller distributional ranges and less diverse sites are expected than created without barriers. β-diversity increased because incorporation of rivers led to creation of smaller species' ranges, lowering average numbers of species at each site and species shared between sites; which in turn reduces covariance between sites and species.

The opposite effect on covariance values is also possible: consider two sites (A and B) with similar species composition, except that A has a few more species than B. If a river acts as a barrier for those few species, they cannot reach A, affecting its local diversity and making the species composition of A and B more similar than they were before. This process directly affects covariance values, and could be the reason for the differences found between P and PR, and S and SR observable in Figure 5.

Seasonality: As explained above, seasonality allows species to invade areas that are environmentally similar in any of the four seasons, increasing the chances of finding suitable areas and being able to expand their distributional range (Janzen 1967). Hence, the effect of seasonality is similar to that of increasing niche breadth: larger ranges, higher α-diversity, and lower β-diversity. The mixture of the effects of these two variables (seasonality and increasing niche breadth) made sites and species fall closer to the zero covariance line in the range-diversity plots (Figures 3 and 4). In

scenario S, environmental conditions are a weaker factor in limiting species'

dispersal since the inclusion of seasonal variation makes it easier for species to

occupy broader areas, especially for those seed points located at sites with high

environmental variability. Note that the spatial patterns of covariances are almost

complementary images when comparing P and S (Figure 5).

History: When the narrowest niche breadth was used, values of β-diversity were

smaller than those obtained for scenarios P and PR (Figure 2), which suggests that

environmental history contributes to reducing local diversity relative to overall

diversity, possibly owing to species extinction of species, while dispersal into areas

not originally accessible, negatively impacts β-diversity. In Figure 6, low between-site

covariance is shown in areas where environmental conditions are unique (Andes and

Patagonia); and species inhabiting these areas are also restricted to them, producing

a very particular local species composition.

Bird dataset: Analysis by sites of the bird distribution polygons obtained from

NatureServe database yielded only positive covariances, suggesting the absence of

sites with unique species composition (i.e., the left-tail in Figure 1C), which are

created by local adaptation in natural systems (Bell 2005). This not-natural behavior

is caused by the generalization to which species' distributions are subject when they

are represented as polygons, ignoring any fine grained associations to environmental

conditions. Similarly, in range-diversity plots (Figure 1B), species are located within a small range of $\bar{s}_i{}^*$ values, in spite of the great variety of their range sizes.

CONCLUSIONS

The framework proposed by Arita *et al.* (2008) was useful for comparing the effects of different processes that affect distributions of species (e.g., niche breadth, physical barriers, seasonality, and history) beyond simple analysis of patterns of species richness, by the measurement of parameters that relate species' ranges to local diversity (range-diversity plots) from the point of view of both sites and species. All factors analyzed had distinctive effects on the artificial biotas which suggest that observed biodiversity patterns are the result of a combination of these processes and probably many others. In spite of the simplicity of the scenarios presented, the expected differentiation between environmentally distinct regions (e.g., the Amazon Basin versus the Andes) is recovered; further, sites with unique species compositions (i.e., left tail of the range-diversity plot by sites) are produced under almost all scenarios.

The level of generalization of the NatureServe bird distributional summaries showed clear effects on range-diversity plots, which suggests that these datasets do not provide an accurate picture of biodiversity pattern. These biases should be taken into consideration in biodiversity analyses, especially if related to conservation efforts, since areas with unique species compositions are particularly under-represented (Jetz et al. 2008). Unfortunately, distributional summaries of bird species at higher spatial resolution were not available for comparison in the present work.

Spatial representation of covariance values was not proposed in the original framework (Arita et al. 2008), but proved to be a useful tool in distinguishing between scenarios with similar statistic parameters, but different geographic concentrations of high and low values of covariance. The simulated patterns under all scenarios coincide with the idea of diversity-driving processes having different weights depending on the region (Ricklefs 2004).

Artificial species created by known parameters (i.e., niche breadth) permitted the analysis of the effects on their distributions owing to the inclusion of other factors involved in shaping species' distributions (i.e., biogeographic barriers, seasonality, and climate history), independently and in tandem. These effects are reflected in the varying species' range size (Nakazawa Submitted-a), species' survival through ecological time (Nakazawa Submitted-b), and, as shown in the present study, distinct biodiversity patterns.

More complicated models should include a set of species with different niche breadths (as opposed to the present work) to approximate natural systems more accurately; however, this task also presents difficulties regarding the selection of niche breadths, the proportion of species with each particular niche breadth (ideally obtained from an empirical distribution), and the geographic location of the species; among others. Two more variables could also be included to create more realistic models: (a) species' dispersal into areas that are suitable but not spatially connected, which would potentially reduce β-diversity values; and (b) interaction between species which would also affect species richness patterns and β-diversity values. Although the effects produced by these two variables are beyond the scope of the

present work, results show that further investigation is needed to assess their importance in shaping biogeographic and macroecologic patterns of biodiversity and species' distributions.

Finally, models intended to simulate species diversity have received increasing and attention in recent years thanks to the inclusion of parameters mimicking natural processes (Rangel et al. 2007). However their accuracy and reality has been evaluated so far by comparing only one aspect of biodiversity (α-diversity patterns). A more interesting and complex model would attempt to re-create both species richness within sites, and association with other species across many sites.

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LITERATURE CITED

Arita, H. T., J. A. Christen, P. Rodríguez, and J. Soberón. 2008. Species diversity and distribution in presence-absence matrices: Mathematical relationships and biological implications. American Naturalist 172:519-532.

Bell, G. 2005. The co-distribution of species in relation to the neural theory of community ecology. Ecology 86:1757-1770.

Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: Size, shape, boundaries, and internal structure. Annual Review of Ecology and Systematics 27:597-623.

Collins, W. D., C. M. Bitz, M. L. Blackmon, G. B. Bonan, C. S. Bretherton, J. A. Carton, P. Chang, S. C. Doney, J. J. Hack, T. B. Henderson, J. T. Kiehl, W. G. Large, D. S. McKenna, B. D. Santer, and R. D. Smith. 2006. The Community Climate System Model version 3 (CCSM3). Journal of Climate 19:2122-2143.

Colwell, R. K., and D. C. Lees. 2000. The mid-domain effect: Geometric constraints on the geography of species richness. Trends in Ecology and Evolution 15:70-76.

Colwell, R. K., C. Rahbek, and N. J. Gotelli. 2004. The mid-domain effect and species richness patterns: what have we learned so far? American Naturalist 163:E1-E23.

Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. American Naturalist 137:27-49.

Forman, R. T. T. 1995. Land Mosaics: The Ecology of Landscapes and Regions. Cambridge, United Kingdom, Cambridge University Press.

Francis, A. P., and D. J. Currie. 1998. Global patterns of tree species richness in moist forests: another look. Oikos 81:598-602.

—. 2003. A globally consistent richness-climate relationship for angiosperms. American Naturalist 161:523-536.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405:220-227.

—. 2003. Structure and dynamics of geographic ranges. Oxford, Oxford University Press.

Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. Ecology 81:2606-2621.

Haffer, J. 1969. Speciation in Amazonian forest birds. Science 195:131-137.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965-1978.

Huston, M. 1994. Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge, United Kingdom, Cambridge University Press.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist 93:145-159.

Janzen, D. H. 1967. Why mountain passes are higher in the Tropics. American Naturalist 101:233-249.

Jetz, W., C. H. Sekercioglu, and J. E. M. Watson. 2008. Ecological correlates and conservation implications of overestimating species geographic ranges. Conservation Biology 22:110-119.

Klopfer, P. H. 1959. Environmental determinants of faunal diversity. American Naturalist 93:337-342.

Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence-absence data. Journal of Animal Ecology 72:367-382.

MacArthur, R. H. 1984. Geographical Ecology: Patterns in the Distribution of Species. New York, Harper & Row Publishers.

McKnight, M. W., P. S. White, R. I. McDonald, J. F. Lamoreux, W. Sechrest, R. S. Ridgely, and S. N. Stuart. 2007. Putting beta-diversity on the map: Broad-scale congruence and coincidence in the extremes. PLoS Biology 5:2424-2432.

Melo, A. S., T. F. L. V. B. Rangel, and J. A. F. Diniz-Filho. 2009. Environmental drivers of beta-diversity patterns in New-World birds and mammals. Ecography 32:226-236.

Nakazawa, Y. Submitted-a. The environmental landscape and its influence on species' distributional patterns. Global Ecology and Biogeography.

—. Submitted-b. A null model for species' distributions and biodiversity patterns, considering climate history and environmental granularity. American Naturalist.

Peterson, A. T., and Á. S. Nyári. 2008. Ecological niche conservatism and Pleistocene refugia in the Thrush-like Mourner, *Schiffornis* sp., in the Neotropics. Evolution 62:173-183.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: A review of concepts. American Naturalist 100:33-46.

Rahbek, C., N. J. Gotelli, R. K. Colwell, G. L. Entsminger, T. F. L. V. B. Rangel, and G. R. Graves. 2007. Predicting continental-scale patterns of bird species richness with spatially explicit models. Proceedings of the Royal Society B 274:165-174.

Rangel, T. F. L. V. B., J. A. F. Diniz-Filho, and R. K. Colwell. 2007. Species richness and evolutionary niche dynamics: A spatial pattern-oriented simulation experiment. American Naturalist 170:602-616.

Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. Ecology Letters 7:1-15.

Ricklefs, R. E., R. E. Latham, and H. Quian. 1999. Global patterns of tree species richness in moist forests: Distinguishing ecological influences and historical contingency. Oikos 86:369-373.

Ridgely, R. S., T. F. Allnutt, T. Brooks, D. K. McNicol, D. W. Mehlman, B. E. Young, and J. R. Zook. 2007. Digital Distribution Maps of the Birds of the Western Hemisphere, version 3.0. Arlington, Virginia, USA, NatureServe.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge, Cambridge University Press.

Waltari, E., R. J. Hijmans, A. T. Peterson, Á. S. Nyári, S. L. Perkins, and R. Guralnick. 2007. Locating Pleistocene refugia: Comparing phylogeographic and ecological niche model predictions. PLoS ONE 2:e563.

Whittaker, R. H. 1972. Evolution and measurements of species diversity. Taxon 21:213-251.

Wiens, J. J., and M. J. Donoghue. 2004. Historical biogeography, ecology and species richness. Trends in Ecology and Evolution 19:639-644.

Table 1. Minimum and maximum covariance for analyses both by sites and by species in the six scenarios (P = present-day conditions; PR = present-day conditions and rivers; S = present-day conditions with seasonality; SR = present-day conditions with seasonality and rivers; H = present-day distributions modeled using climate history; and B = bird distributions from NatureServe) at the three environmental similarity thresholds (niche breadth); note that the similarity thresholds do not apply to the latter scenario.

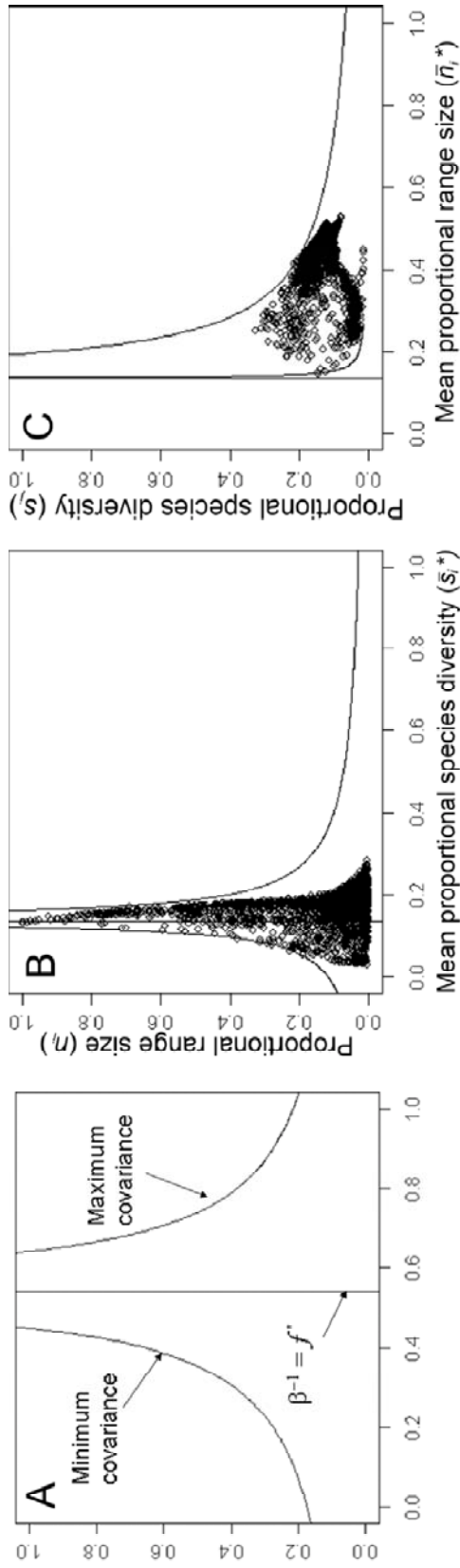|		By site			By species		
		5%	10%	20%	5%	10%	20%
P	Min	-0.0005	-0.0119	-0.0542	-0.0007	-0.0141	-0.0394
	Max	0.0072	0.0619	0.1015	0.0073	0.0519	0.0637
PR	Min	-0.0003	-0.0063	-0.0451	-0.0006	-0.0099	-0.0452
	Max	0.0067	0.0513	0.0988	0.0067	0.0495	0.0873
S	Min	-0.0302	-0.0230	-0.0047	-0.0229	-0.0107	-0.0031
	Max	0.0784	0.0605	0.0283	0.0486	0.0254	0.0069
SR	Min	-0.0358	-0.0237	-0.0061	-0.0487	-0.0201	-0.0018
	Max	0.1228	0.1066	0.0539	0.0798	0.0303	0.0072
H	Min	-0.0015	-0.0265	-0.0396	-0.0032	-0.0181	-0.0272
	Max	0.0169	0.0779	0.0823	0.0167	0.0693	0.0524
B	Min	0.0018			-0.0158		
	Max	0.0598			0.0266		

Figure 1. A: Range-diversity plot: x- and y-axis correspond to the mean species diversity ($\bar{s}_i^*$)

and the proportional range size (n_i) in the analysis by species, while the axes for the analysis by

sites are mean proportional range size ($\bar{n}_j^*$) and proportional species diversity (s_j). The

proportional fill of the matrix (f^*) indicates the general position of the cloud of points, while the

maximum and minimum covariance set the limits of the areas where sites or species are

plotted. B: Range-diversity plot constructed with bird distribution maps from NatureServe,

analyzed by species; points in the graph represent all 2639 bird species included in the

analysis. C: Range-diversity plot constructed with bird distribution maps from NatureServe,

analyzed by sites; points represent all 1925 squares used to sample the study area (sites).
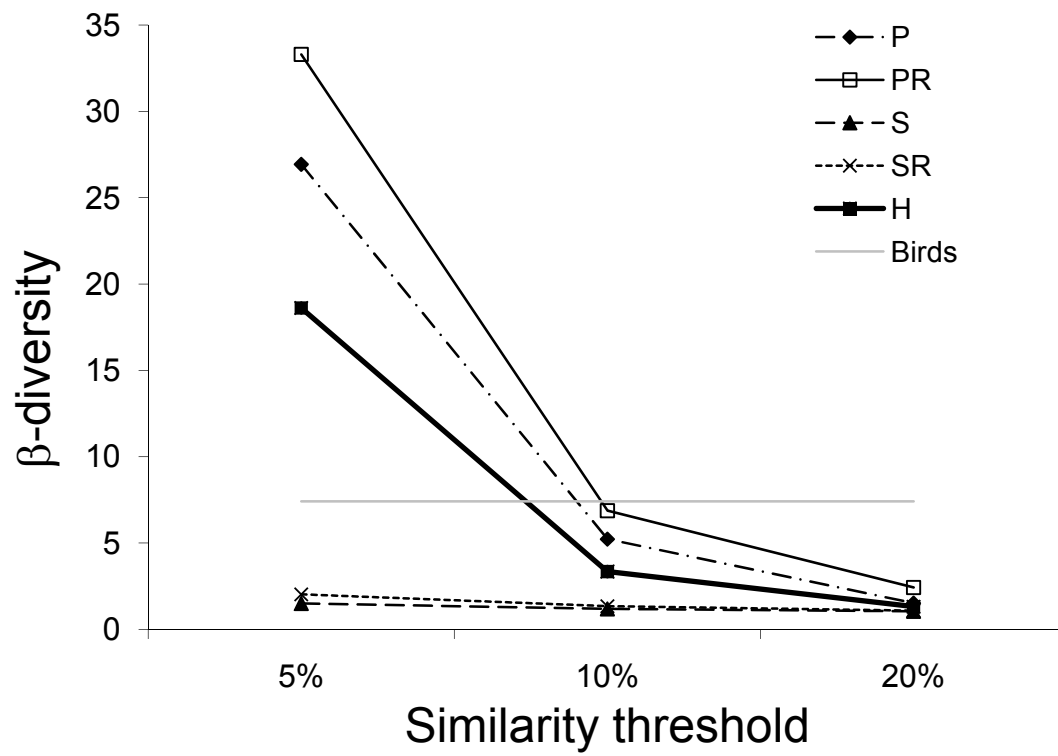
Figure 2. β-diversity values for all six scenarios (letters are the same as in Table 1) and their changes as niche bread increases.
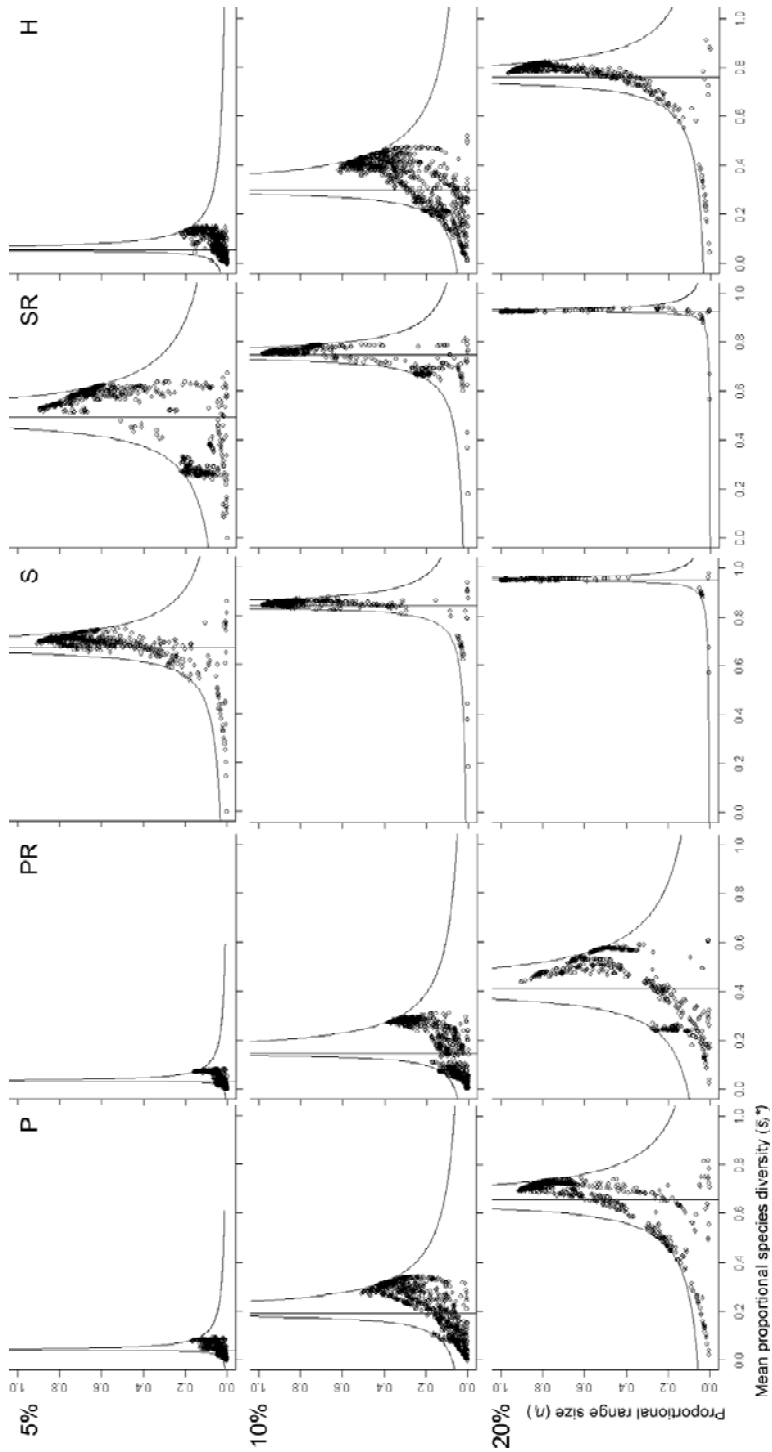
Figure 3. Range-diversity plots from the analysis by species for the five modeled scenarios (letters are the same as in Table 1), using three environmental similarity thresholds (5%, 10% and 20%), which define three levels of niche breadth.
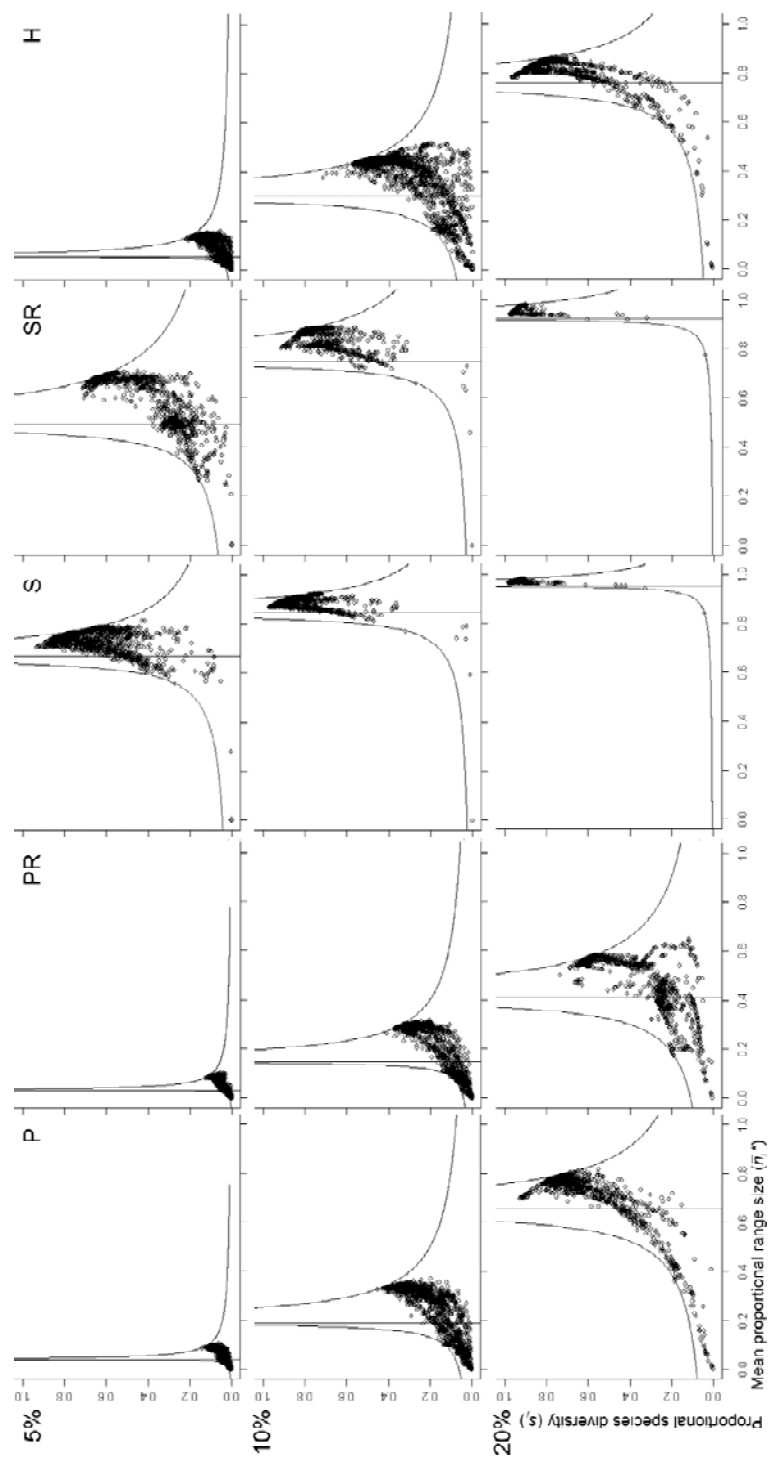
Figure 4. Range-diversity plots from the analysis by sites for the five modeled scenarios (letters are the same as in Table 1), using three environmental similarity thresholds (5%, 10% and 20%), which define three levels of niche breadth.
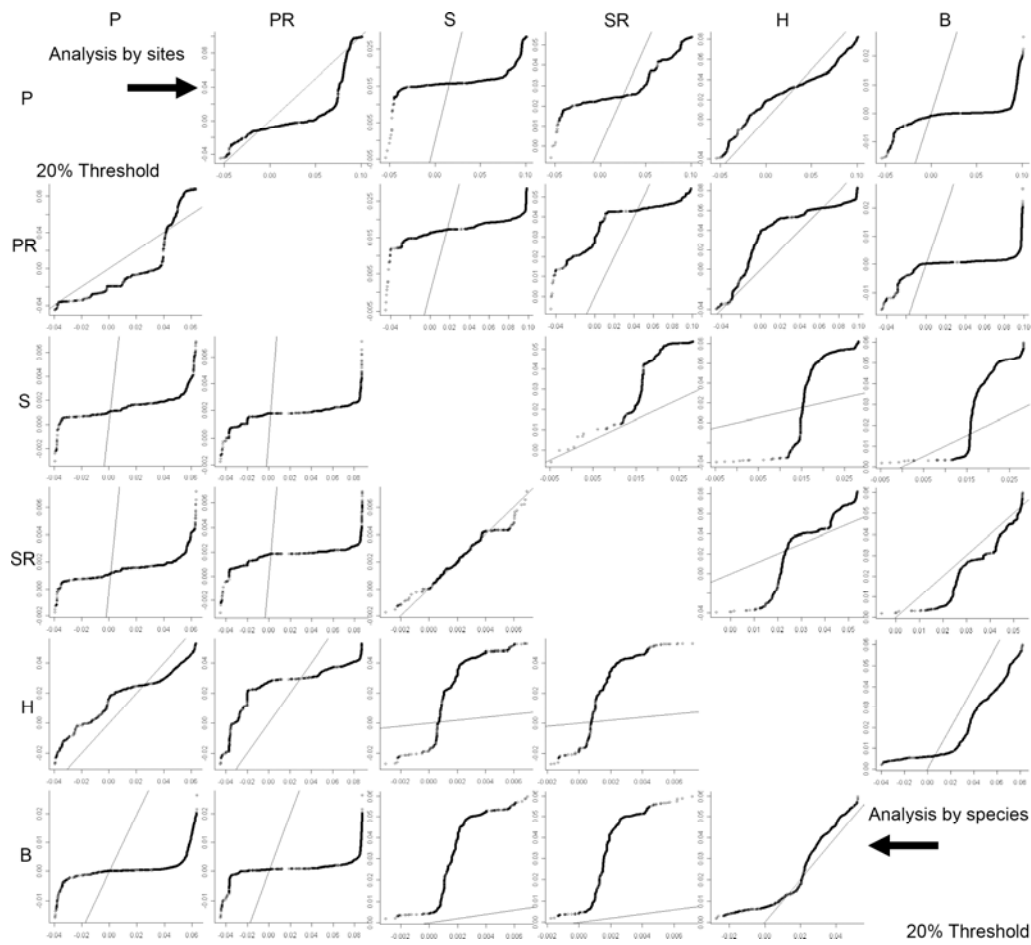
Figure 5. QQ-plots comparing covariance distributions for all modeled scenarios (letters refer to Table 1) using the broadest niche level. The diagonal line in each plot shows the expected trend when both distributions are exactly the same.
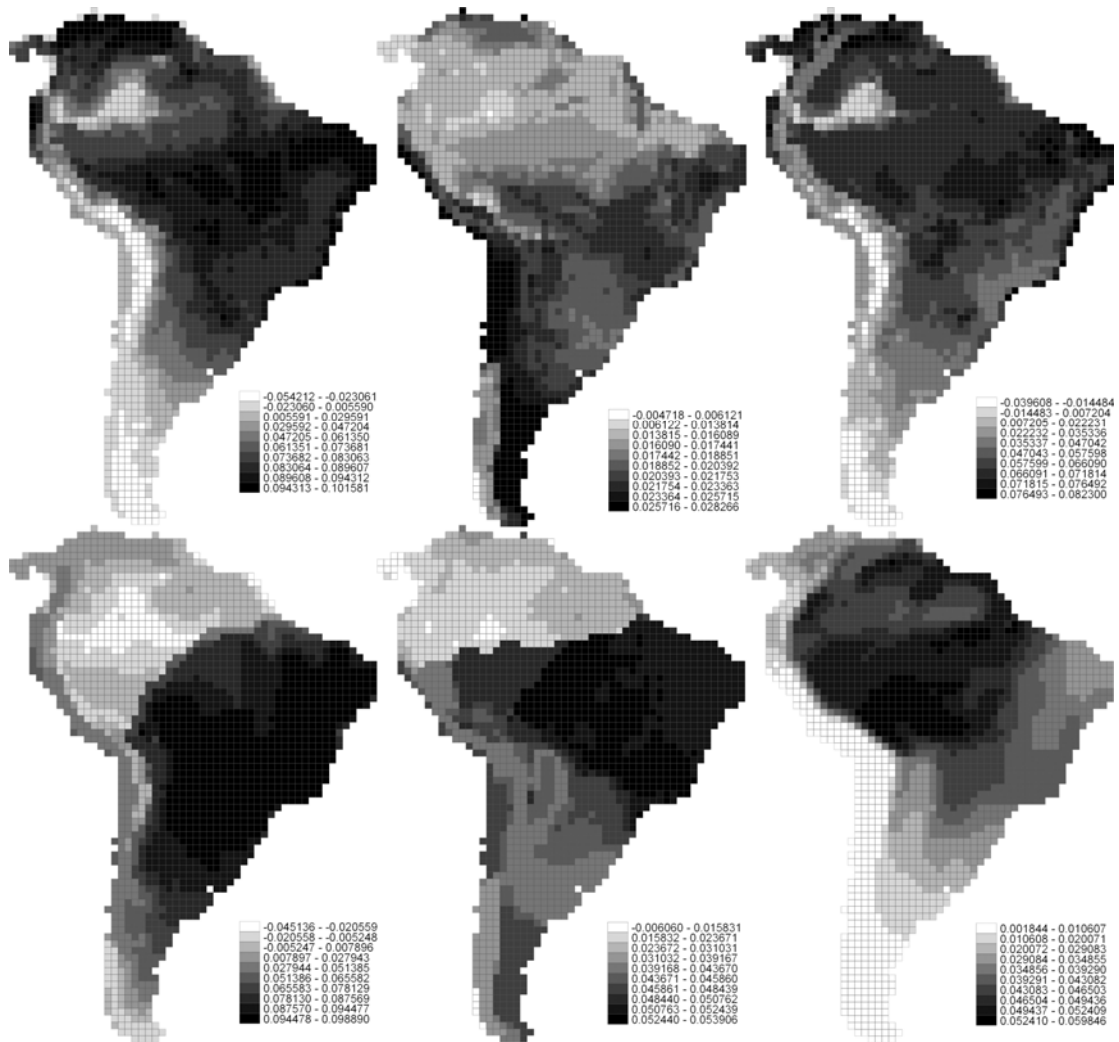
Figure 6: Covariance maps for all simulated scenarios (P, PR, S, SR and H; letters are the same as in Table 1) using the highest level of niche breadth (20%), and covariance calculated for bird species (B). Low and high covariance are shown in light and dark shades of gray, respectively. Note that classes are not equivalent between maps.