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RESEARCH PAPERS

# Effects of neutrality, geometric constraints, climate, and habitat quality on species richness and composition of Atlantic Forest small-mammals

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## ABSTRACT

**Aim** To compare the fit of models of climate, habitat quality, neutral processes, and geometric constraints to species richness and composition of small mammal assemblages.

**Location** The South American Atlantic Forest biome.

**Methods** Using neutral models and mid-domain effect models, we simulated species spread in a spatially explicit array of grid cells representing the Atlantic Forest domain. We compared empirical patterns of species richness and composition with predictions of the neutral and mid-domain effect models. We also modeled individual species responses to climatic conditions and forest integrity, a measure of habitat quality.

**Results** Habitat quality was the single best predictor of local species richness ($\alpha$-diversity), but was a poor predictor of local species composition and of the decay in species similarity with distance ($\beta$-diversity). The neutral and mid-domain models generated very similar predictions, and were better predictors of species composition than of species richness. Climate variables were also strongly associated with overall species composition, but not with species richness.

**Main Conclusions** The species richness of small-mammal assemblages in the Atlantic Forest is best explained by variation in habitat quality. In contrast, the composition of small-mammal assemblages is best explained by models of limited dispersal (neutral and mid-domain) and effects of climate on local species composition. Collectively, these results suggest that regional patterns of species richness may be uncoupled from patterns of species composition. Both species richness and composition should be considered when evaluating the predictions of neutral and mid-domain effect models, and of correlations of community structure with climatic or habitat variables.

### Keywords

**$\alpha$-diversity, $\beta$-diversity, cellular automata, dispersal limitation, distance-decay, Generalized Linear Model, habitat loss, mid-domain effect.**

## INTRODUCTION

At a variety of spatial scales, species richness and species composition are often correlated with measures of area (Storch *et al.*, 2012), contemporary climate (Hawkins *et al.*, 2003), habitat quality (Fahrig, 2003), and isolation by distance (Svenning & Skov, 2007). However, teasing apart the mechanisms underlying these correlations and attributing them to historical (Haffer, 1985; Carnaval & Moritz, 2008) versus contemporary factors (Hawkins *et al.*, 2003) is challenging.

Studies of habitat quality, climatic factors, and geometric constraints have usually focused on species richness (Fahrig, 2003;

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Hawkins *et al.*, 2003; Rangel & Diniz-Filho, 2005), whereas studies of dispersal and neutral processes have usually focused on species-abundance relationships (McGill *et al.*, 2006; Rosindell & Cornell, 2013), and distance-decay patterns (Smith & Lundholm, 2010; Diniz-Filho *et al.*, 2012). When these patterns are tested in isolation for single models, they may not be informative. For example, patterns of rank abundance distributions have poor discriminatory power for distinguishing niche and neutral processes (McGill *et al.*, 2006). Similarly, it may be difficult to distinguish effects of environmental filtering from effects of dispersal on distance-decay relationships (Smith & Lundholm, 2010).

Several studies in the Atlantic Forest biome of South America have explained the high species diversity in this forest by historical events associated with the limited species dispersal (Haffer, 1985; Carnaval & Moritz, 2008; de la Sancha *et al.*, 2014). Nevertheless, other processes such as species adaptation to contemporary climate (Carnaval & Moritz, 2008; Carnaval *et al.*, 2014), habitat availability (Chiarello 1999; Tabarelli *et al.*, 2010), and the geometry of the Atlantic Forest (Prevedello *et al.*, 2013) also contribute to the contemporary distribution of species.

In this study, we compiled data from 52 published studies on the species richness and composition of small mammals sampled across the Atlantic Forest biome of South America. We simultaneously compared the predictions of four models – contemporary climatic, habitat quality, neutral, and geometric constraints – on three patterns of species distribution: local species richness, species composition, and distance-decay relationships. We compared the relative performance of each of these models to each other, as well as to a null model that incorporated only sampling effects.

## METHODS

### Study site

The Atlantic Forest extends from the northeast coast of Brazil to northern Argentina. This biome harbors several endemic and patchily distributed species (Costa *et al.*, 2000), which might suggest that dispersal limitation was an important determinant of species distributions. In agreement with models of random dispersal (Economo & Keitt, 2010) and species geometric constraints (Jetz & Rahbek, 2001), Costa *et al.* (2000) found that areas with higher small-mammal diversity are located in the central parts of the Atlantic Forest. Nevertheless, there is also evidence that small mammal composition in the Atlantic Forest is associated with climatic conditions (Carnaval *et al.*, 2014; de la Sancha *et al.*, 2014). Moreover, the Atlantic Forest is a highly perturbed region (Ribeiro *et al.*, 2009), and contemporary habitat quality could have a strong effect on local species richness and composition (Fahrig, 2003).

The data compiled for this study were collected across the entire area recognized as the Atlantic Forest biome (Fig. 1). This biome encompasses an extent of 102,012 km$^2$, of which only 7.9% is still intact. Habitat types in intact areas include rainforests, mixed (*Araucaria*) moist forests, semideciduous forests, dry forests, and upland grasslands. Rainforests tend to occur near the coast, whereas semideciduous and dry forests occur far from coast. Mixed forests are common in the south of the Atlantic Forest (Leite, 2002). The climate is moist tropical and subtropical, without a well-defined dry season, and with annual mean temperatures above 15 °C (Leite, 2002).

### Data collection

We compiled a database of 52 studies from the primary literature in which small mammals were sampled in the Atlantic Forest (Table S1 in Supporting Information). We used the Google Scholar search tool with the keywords 'small mammal', 'marsupial', 'rodent', 'community', 'composition', 'richness', 'diversity', and 'Atlantic Forest' (Table S1).

For inclusion in our database, we established a minimum sampling effort of at least 1000 trap-nights, 6 months of field work, and use of wire and/or Sherman live-traps installed on the ground or understory level of the forest. Studies area ranged from 5 to 185,000 ha ($\bar{x} = 16{,}295$), with sampling effort from 600 to 64,000 h of trapping ($\bar{x} = 9178$). The distance between sites ranged from 31 to 3249 km ($\bar{x} = 1026$). The studies locations ranged from 32°33′ S to 8°15′ S and from 54°58′ 12′ ′ W to 35°4′ 48″ W. The number of species recorded in each study ranged from 1 to 27 ($\bar{x} = 8.16$). From each selected survey, we obtained local species composition. The species recorded from 75 surveyed locations were aggregated into 26 2 × 2° grid cells for analysis (Fig. 1). To account for possible sampling effects, we included the number of trapping hours in each grid cell as a covariate in our models (detailed description below).

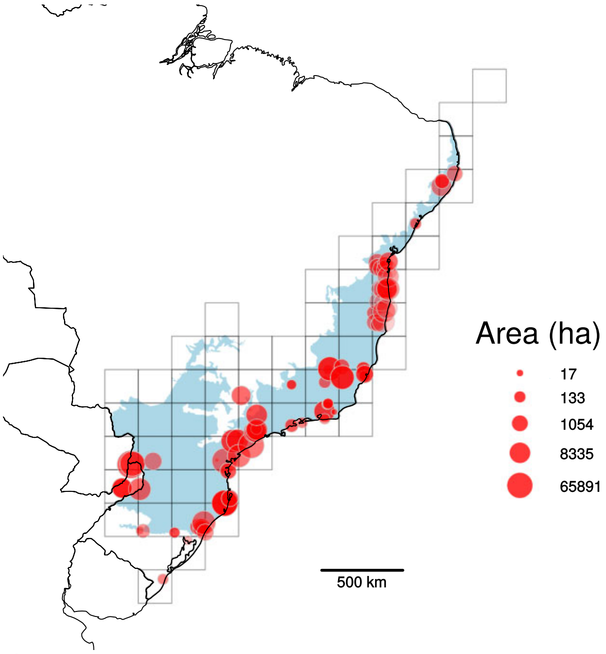

**Figure 1** Map of the Atlantic Forest (AF) showing the original sampling points (circles) and the 55 grid cells encompassing the entire AF. The diameter of each circle is proportional to the logarithm of sampled area.

In rasters of 2.5 arc minutes, we also compiled the 19 environmental variables available in Bioclim (http://www.worldclim.org/bioclim): annual mean temperature (1), mean diurnal temperature range (2), isothermality (3), temperature seasonality (4), maximum and minimum temperature of the warmest and coldest months (5 and 6), temperature annual range (7), mean temperature of the wettest, driest, warmest, and coldest quarters (8–11), annual precipitation (12), precipitation of the wettest and driest months (13 and 14), precipitation seasonality (15), and precipitation of the wettest, driest, warmest, and coldest quarters (16–19). We then averaged the measure of each environmental variable within each 2 × 2° grid cell. Because most of the climatic variables are correlated with one another, we summarized them with a Principal Component Analysis. The first principal component axis was used as a predictor variable in all models. We present the results using individual climatic variables in the supplemental material (Figs S1–S5).

Habitat quality was quantified with information available from each study. We classified forest status of each study on a scale from 1 to 5 (1 = highly disturbed forest, including clearings, 2 = secondary forest, 3 = disturbed primary forest, 4 = conserved primary forest with patches of old secondary forest; 5 = conserved primary (old growth) forest). Areas of primary forest were characterized by an intact canopy with no evidence of previous clearing (Eiten, 1983); secondary forests were characterized by evidence of regeneration after clearing and land use (Eiten, 1983; Veloso *et al.*, 1991). We calculated the average habitat score for the studies that were located in each grid cell.

## Analysis

The number of species encountered in each grid cell (S), and the pairwise similarity in species composition, as measured by the Jaccard similarity index, were used as response variables. The Jaccard similarity index between two grid cells takes into account the similarity in species identity and the number of shared species between the grid cells (Baselga, 2012). However, the Jaccard index is also affected by differences between sites in species number, and may be correlated with patterns of species richness as well as species composition. To investigate the changes in species identity between two grid cells independently from differences in species richness, we partitioned the Jaccard similarity index into components of turnover and nestedness (Baselga, 2012), and used the turnover component as a response variable.

### *Dispersal-based models*

To estimate the influence of dispersal limitation on species richness (S) and composition (Jaccard and Jaccard turnover indices), we created a network of interconnected grid cells representing the Atlantic Forest (Fig. S6). This network was used to estimate the flux of species or individuals among grid cells in simulation models. Two models were used to recreate the species distribution under dispersal alone: the spreading dye model (Jetz & Rahbek, 2001), and the neutral model (Economo & Keitt, 2008).

In both models, the entire area comprising the Atlantic Forest was divided in 55 2 × 2° grid cells, including the 26 for which small mammal data were available (Fig. 1). In the spreading dye model, the number of grid cells occupied by each small mammal species was recorded. The occurrence of each species for the entire Atlantic Forest (n = 55) was estimated from the grid cells in which small-mammal data were available (n = 26). One of the 55 grid cells was randomly selected and the species occurrence was spread from the selected cell into neighboring cells until the original number of occupied grid cells was achieved. Each cell had up to eight neighbors (Moore neighborhood; Fig. S6), and the model was bounded by the domain of the 55 grid cells. This procedure was repeated 10,000 times for the 64 species.

The neutral model was started with a single ancestral species occupying all 55 grid cells. In each generation, new species were added in each cell by point speciation with probability $\nu$, which was constant across all cells (see Economo & Keitt 2010 for more details). The constant $\nu$ represents the probability of an individual speciating, but could also be interpreted as the probability of adding a new species by immigration and simultaneously losing a single individual of a resident species. Both interpretations impose a zero-sum game on the total number of individuals. To model the probability of dispersal, we allowed a cell to be colonized only from an occupied neighboring cell (Moore neighborhood, Fig. S6), with all grid cells having the same migration rate ($m$). The local community size (number of individuals) was set the same for all grid cells ($N = 100$). The model was run for multiple generations (usually more than 30,000), until the $\alpha$-diversity within grid cells (Probability of Interespecific Encounter; Hurlbert, 1971) and $\beta$-diversity between grid cells (Morisita-Horn similarity) reached a steady-state.

The neutral model of Economo & Keitt (2008) is probabilistic and does not require the simulation of each individual in the metacommunity. This model allowed us to investigate thoroughly the parameter space of $m$ and $\nu$. However, because the Economo & Keitt (2008) model does not generate species identities in different sites (but only the probability of two individuals selected at random in a pair of sites being from the same species) it does not allow one to calculate statistics based on composition (such as the Jaccard similarity index).

Nevertheless, it is possible to calculate the Morisita-Horn similarity matrix between all possible pairs of sites based on the probability of ancestry of individuals. Using the Limited-memory Broyden-Fletcher-Goldfarb-Shanno Box-constrained (L-BFSG-B) optimization algorithm (Byrd *et al.*, 1995), we estimated $m$ and $\nu$ to maximize the correlation between the Morisita-Horn index of the neutral model and the Jaccard index of the observed data. These indices are usually highly correlated (Krasnov *et al.*, 2005; Chao *et al.*, 2006). To confirm this approach, we used the optimized parameters ($m$ and $\nu$) to simulate a single community with a burn-in of 30,000 generations, and then ran the model with 1000 time steps for 10,000 different simulations. The mean of the 10,000 simulations was used to calculate the Jaccard similarity index. The correlation between the Morisita-Horn index of the probabilistic model and the Morisita-Horn index of the simulated model was 0.9998. We used the species richness, the Jaccard similarity index, and the turnover component from the Jaccard similarity index from this simulation model as the predicted values from the optimized neutral model.

### Environmental models

To test the association of species diversity with the climatic and habitat quality variables, individual logistic regressions were fitted for each species against the climatic and habitat quality variables. We refer to these models hereafter as the climatic and habitat models.

The logistic model estimates the effect of a predictor variable on the species probability of occurrence. These probabilities can then be used to estimate the effect of the predictor variable on the overall species richness (S) and composition.

To calculate the expected species richness and Jaccard pairwise similarity index based on the climatic and habitat models, the distribution of each species was simulated in a spatially explicit model (Rahbek *et al*., 2007). For each species, we assigned randomly species occurrences (1 s) in grid cells based on the probabilities of occurrence predicted by a climatic or habitat variable. This procedure was performed independently for each grid cell, and the observed species occurrences were not preserved. Note that this model does not require the species to have contiguous ranges as in the spreading dye model. The simulation was replicated 10,000 times to calculate the mean species richness in grid cells, and the Jaccard index and turnover between each pair of grid cells. For species richness, similar results were obtained by summing the probability of occurrence of all species in a grid cell, as predicted by an individual climatic or habitat quality variable in logistic regressions.

The probability of species occurrence estimated from logistic models can be affected by the species prevalence (Real *et al*., 2006). To account for the effect of species prevalence in the estimation of the species probability of occurrence, we rescaled the probabilities obtained in logistic regressions (Real *et al*., 2006), and used these probabilities to estimate species richness and composition in our models. The results obtained by using the rescaled probabilities were similar to the results obtained using the raw probabilities, and the results from the rescaled probabilities are shown as Supporting Information (Table S2).

Additionally, we fit a linear regression of S, and a distance-based RDA that used the Jaccard index and the turnover component of the Jaccard index, against the raw environmental variables. The results of these tests were very similar to those using the individual logistic regressions and are presented in the supplemental material (Figs S3–S5).

### Model comparisons

We compared the four simulation models (spreading dye model, neutral model, climatic model, and habitat model) by their Mean Square Error (MSE). The MSE was calculated as the sum of the squared bias and the model variance (Gotelli *et al*., 2009):

$$\sum (bias)^2 = \sum_{i=1}^{c} (O_i - E_i)^2,$$

$$\sum (VAR) = \frac{1}{(R-1)} \sum_{k=1}^{R} \sum_{i=1}^{c} (U_{ki} - E_i)^2, \text{ and}$$

$$\sum (MSE) = \sum (bias)^2 + \sum (VAR),$$

where **O** represents the vector of observed values for each grid cell $i$, **E** is a vector of the mean expected values in the simulation model for each grid cell $i$, $U_{ki}$ represents the value obtained in the $k$th simulation for the cell $i$, and $R$ is the number of simulations run for each model.

Additionally, we ran individual linear regression models for species richness, and distance-based RDA (dbRDA) analyses for the Jaccard index of species composition and the turnover component of the Jaccard index, using as explanatory variables the predicted values from the spreading dye, neutral, climatic, and habitat models. Because sampling effort varied across the study area, and had the potential to affect both species richness and composition, we included the logarithm of the number of trap hours as a single predictor variable into the regression and dbRDA models. We then used the residuals from these models as response variables representing species richness and composition. At regional and local spatial scales, species richness and sampling effort often have an asymptotic relationship, which was nearly linearized by log transforming the number of trap hours. For all model comparisons, we obtained $r^2$ and $P$-values from the regression and RDA models.

### Distance-decay analyses

To compare the effects of geographical isolation and environmental distance on the Jaccard similarity in species composition and the turnover component of similarity, we calculated the geographical distance (matrix D), and environmental distance (matrices H and C for habitat and climatic variables, respectively) between all pairs of grid cells. We then performed simple and multiple generalized linear models (GLMs) with log links on distance matrices to estimate the relationship between the similarity in species composition and the geographical and environmental distances (Millar *et al*., 2011).

Because the Jaccard similarity is a proportion (proportion of shared species), the error of this model was fit with a binomial distribution (Millar *et al*., 2011). $P$-values for the GLMs were calculated by permuting the rows and columns of the Jaccard similarity matrix 999 times. In each permutation, GLM coefficients were recorded, generating a null distribution of coefficients. Because we expect a negative relationship between the similarity in species composition and geographic, climatic, and habitat distances, $P$-values were calculated as the number of times that GLM coefficients were lower than observed + 1 divided by the number of permutations + 1 (one-tailed test).

Table 1 Fit of the climatic, habitat quality, spreading dye, and neutral models for species richness and composition. Species composition was measured as the Jaccard similarity index and the turnover component of the Jaccard similarity index (Baselga, 2012). BIASsq: Sum of squared bias; VAR: sum of model variance; MSE: sum of mean square errors (BIASsq + VAR). See main text for details on the BIASsq and VAR calculations; $r_{partial}^2$: Explained variance after removing the effects of log transformed trapping hours on the response variables. $r^2$ and *P*-values were calculated from regression models. *P*-values were corrected for sampling effort by removing the effects of log transformed trapping hours on the response variables before analysis.

| Response variable | Explanatory model | BIASsq | VAR | MSE | *P* | $r^2$ | $r_{partial}^2$ |
|---|---|---|---|---|---|---|---|
| Richness | Climatic | 1394.69 | 353.04 | 1747.73 | 0.47 | 0.01 | 0.01 |
| | Habitat | 1038.90 | 197.73 | 1236.63 | 0.019 | 0.21 | 0.07 |
| | Spreading dye | 1262.47 | 202.87 | 1465.34 | 0.624 | 0.09 | 0.01 |
| | Neutral | 1597.73 | 225.00 | 1822.73 | 0.459 | 0.09 | 0.01 |
| Composition (turnover + nestedness) | Climatic | 4.97 | 2.98 | 7.94 | 0.005 | 0.22 | 0.20 |
| | Habitat | 3.60 | 3.40 | 7.00 | 0.472 | 0.10 | 0.07 |
| | Spreading dye | 6.64 | 2.10 | 8.75 | < 0.001 | 0.27 | 0.23 |
| | Neutral | 5.91 | 4.06 | 9.97 | < 0.001 | 0.27 | 0.24 |
| Composition (turnover) | Climatic | 5.10 | 2.73 | 7.83 | 0.005 | 0.39 | 0.38 |
| | Habitat | 3.65 | 3.12 | 6.77 | 0.437 | 0.11 | 0.11 |
| | Spreading dye | 6.93 | 1.62 | 8.55 | < 0.001 | 0.43 | 0.42 |
| | Neutral | 6.23 | 3.83 | 10.06 | < 0.001 | 0.43 | 0.42 |

All analyses were conducted in R (R Development Core Team, 2013, v. 3.0.2). Most of the summary statistics calculations were implemented by the authors, and are available at http://www.uvm.edu/~cddambro. We used the package Vegan (Oksanen *et al.*, 2008) for the remaining analyses.

## RESULTS

### Patterns of species richness

All the models had a poor fit to species richness (Table 1; Figs 2 and S3). The maximum $r^2$ was only 0.21 for the habitat model, which had the lowest mean square error, variance, and bias. Both the neutral model and the spreading dye models generated the familiar peak of species richness in the middle of the domain of the Atlantic Forest, whereas the empirical peak of species richness occurred in two disjunct coastal grid cells (Fig. 2).

### Patterns of species composition

Species composition (measured as principal coordinates of the Jaccard similarity matrix in dbRDA analyses) was best fit by the neutral model ($r^2 = 0.27$), the spreading dye model ($r^2 = 0.27$), and the climate model ($r^2 = 0.22$), but was poorly fit by the habitat model ($r^2 = 0.10$; Table 1; Figs 3 and S4). Most of the variation (24 %) in species composition was represented in the first principal coordinates axis of dbRDA. Species composition in the first principal coordinates axis was well-fit by the neutral model ($r^2 = 0.77$), the spreading dye model ($r^2 = 0.75$), and the climate model ($r^2 = 0.63$), but was poorly fit by the habitat model ($r^2 = 0.04$).

The analysis of the turnover component of the Jaccard similarity index generated results that were similar to the analysis of overall species composition (Table 1). However, the explanatory power of the climate ($r^2 = 0.39$), spreading dye ($r^2 = 0.43$), and neutral ($r^2 = 0.43$) models was higher than for the analysis of overall species composition (Table 1).

The four models generated contrasting predictions for the distance-decay relationship of species similarity versus geographic distance. The spreading dye and neutral models predicted a steep distance-decay function, whereas the climate model predicted a linear decay and the habitat model predicted no decay with distance (Fig. 4). The predictions of all four models differed from the empirical best-fit GLM exponential curve.

The similarity in species composition between two grid cells was associated with the geographical distance and climatic dissimilarity between cells ($b_{GLM} = -0.29$ and $b_{GLM} = -0.12$, respectively; Table 2). However, only geographical distance was correlated with the similarity in species composition when all predictor variables were included into a single model ($b_{GLM} = -0.23$; Table 2). Habitat quality was not significantly associated with the similarity in species composition in simple or multiple GLM models ($b_{GLM} \le |0.02|$; Table 2). Similar results were found when the turnover component in the Jaccard similarity index was separated from the nestedness component.

## DISCUSSION

### Patterns of species richness

At the biogeographic scale, species richness of many taxa is well-correlated with climate variables, especially temperature and precipitation (Hawkins *et al.*, 2003). At the regional scale of the Atlantic Forest, the best predictor of small-mammal species richness was a simple measure of habitat quality (Table 1; Fig. 2). Neutral or mid-domain effect models did not predict richness very well. Although our implementation of the neutral

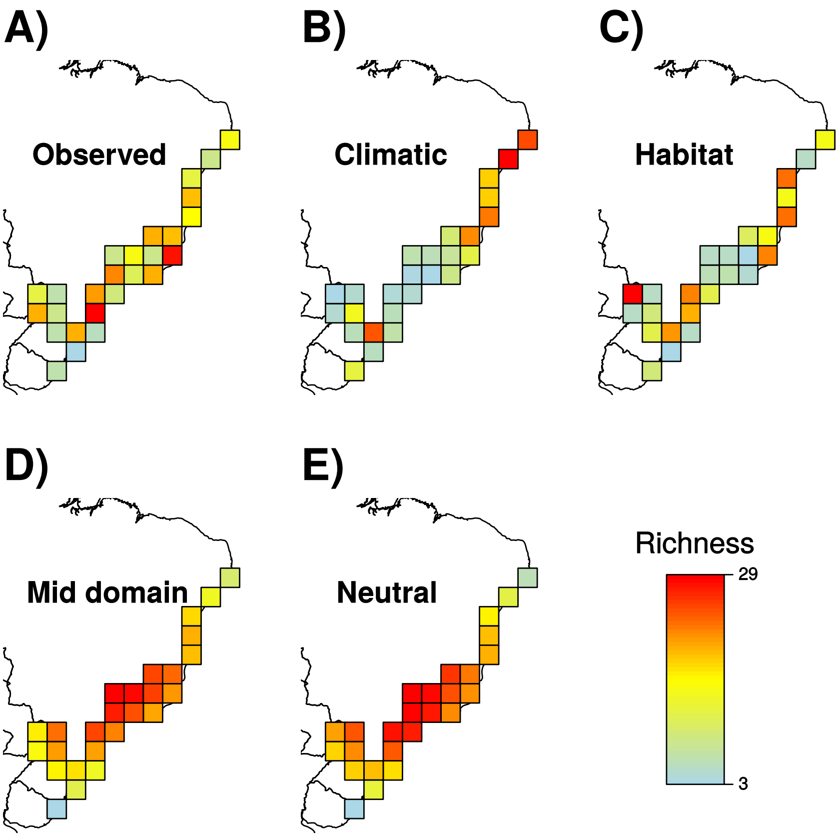

Figure 2 Observed and predicted richness of the small mammal species in the Atlantic Forest. (a) Observed, (b-c) Predicted richness from logistic regression models of climate variables (b) and habitat quality (c), (d-e) Predicted richness from the spreading dye model (d) and the neutral model (e). Open cells in (e) represent areas included in the models but where actual small-mammal data were not available. The spreading dye model and the neutral model predicted highest species richness in the center of the domain, but the two grid cells with the highest species richness were in two disjunct coastal grid cells. Habitat quality was the best predictor of species richness.

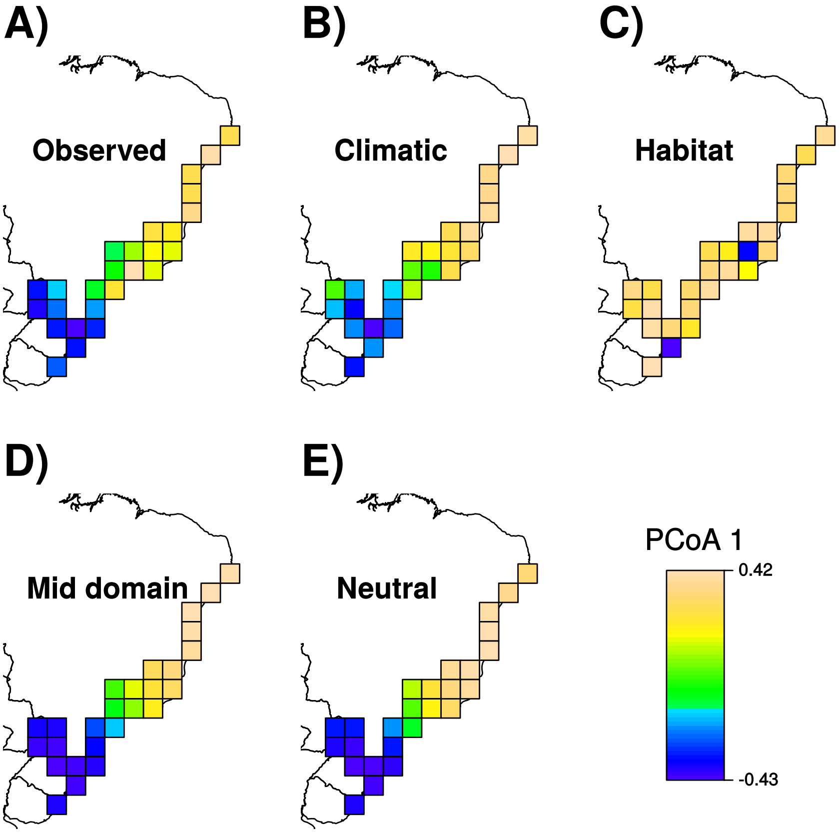

Figure 3 Observed and predicted composition of small mammal species in the Atlantic Forest. The composition was measured using the turnover component of the Jaccard similarity index (Baselga, 2012), and analyzed using a distance-based RDA model. Similar colors represent similar composition of species. (a) Observed, (b-c) Predicted composition from logistic regression models of climate variables (b) and habitat quality (c), (d-e) Predicted composition from the spreading dye model (d) and the neutral model (e). Open cells in (e) represent areas included in the neutral model but where actual data were not available. The climatic, spreading dye, and neutral models performed equally well in explaining species composition in the Atlantic Forest.

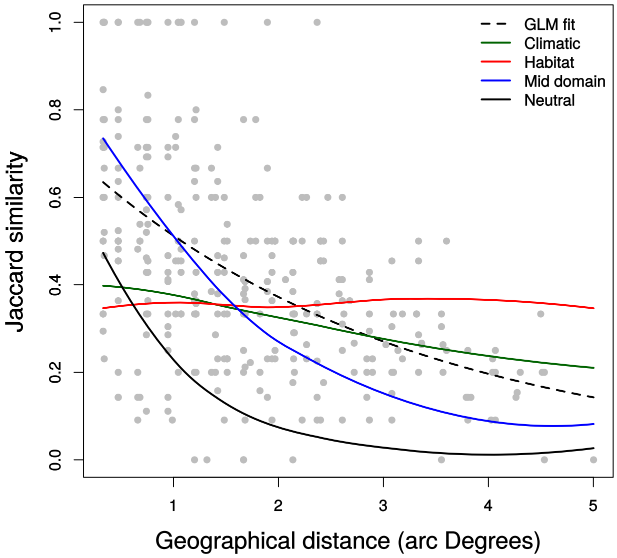

Figure 4 Decay in the similarity of species composition with geographical distance. The similarity in species composition was measured by the Jaccard similarity index between all pairs of grid cells (grey circles). The similarity was regressed against geographical distance, climatic and habitat quality distances using a Generalized Linear Model with binomial errors and a log link function. Habitat quality and climatic variables did not predict the exponential decay with geographical distance. The spreading dye model and the neutral model predicted a much steeper decay with distance than did the GLM.

model was optimized to account for species composition, the fit did not improve when we optimized it for species richness ($r^2 = 0.11$ vs 0.09; results not shown). These results suggest that, in the absence of other factors, dispersal limitation and geometric constraints did not have a strong influence on species richness.

Our index of habitat quality in each grid cell quantifies fragmentation and forest loss, and our results are consistent with many other empirical and theoretical studies on these processes (Fahrig, 2003). Most species extinctions after perturbations occur directly from the loss of habitat area (Fahrig, 2003) and indirectly from changes in the microclimate of fragments (Saunders *et al.*, 1991). The reduction of population sizes by the fragmentation of patches also leads to stochastic extinctions, because small populations have a higher chance of declining to zero (May, 1973).

For entire communities of long-lived organisms, stochastic extinctions following perturbations can take hundreds or even thousands of years to significantly modify the composition and overall diversity (Diamond, 1972; Kuussaari *et al.*, 2009; Halley & Iwasa, 2011). Habitat loss usually has a stronger effect on species diversity (Fahrig, 2003), and the degradation of the Atlantic Forest probably has affected small mammal communities by the immediate loss of habitat area. Therefore, extinction debts (Tilman *et al.*, 1994) might still exist, which could lead additional species losses in the Atlantic Forest. Although forest fragmentation and habitat loss are important in the Atlantic Forest, the best-fitting model still explained only 21% of the variance in species richness (Table 1). Indeed, sampling effort alone (logarithm of number of trapping hours) explained more variation than did habitat quality ($r^2 = 0.40$), although the residual effect of habitat quality is still significant when the sampling effect is controlled for ($P = 0.02$).

Our implementation of the neutral model did not allow for variation in the species abundances across grid cells, so it could not incorporate the possibility of higher extinction rates in grid cells with low habitat quality. The inclusion of habitat quality as a proxy for species abundances in the neutral model could allow the estimation of the immediate (Dornelas, 2010) and long term (Halley & Iwasa, 2011) effects of habitat loss in small mammal communities. Similarly, in the spreading dye model, the probability of occupancy of a grid cell could be modeled as a function of habitat quality (Rahbek *et al.*, 2007).

### Patterns of species composition

Surprisingly, habitat quality was not associated with the composition of small mammals in the Atlantic Forest. Usually, rare and specialized species are more affected by environmental perturbations than are common species, and such perturbations can lead to biotic homogenization by favoring a few dominant species in low-quality habitats (McKinney & Lockwood, 1999). However, in the Atlantic Forest, pairs of geographically distant grid cells supported distinct sets of species even when these cells were both comprised of low-quality habitats. Moreover, there was not a single dominant species occupying all low-quality habitats in the Atlantic Forest.

Dispersal limitation and diversification, as simulated in the neutral model, could cause disjunct patches with similar environments to evolve distinct sets of species. This type of model is potentially realistic for the Atlantic Forest small-mammals, which exhibit a high degree of endemism, with many rare and patchily distributed species (Costa *et al.*, 2000). However, our neutral and spreading dye models do not assume the presence of forest refugia or high diversification areas, which are commonly invoked to account for diversity in the Atlantic Forest (Haffer, 1985; Carnaval & Moritz, 2008; de la Sancha *et al.*, 2014).

Climatic conditions were also strongly correlated with the composition of species in grid cells. Along with dispersal limitation imposed by geographical distance, the climatic conditions of a grid cell could limit the immigration and establishment of species adapted to other climates. Recently, differences in climatic conditions between the northern and southern parts of the Atlantic Forest have been associated with changes in species composition for many taxa (Carnaval *et al.*, 2014). However, our results suggest that similar patterns could be generated by simple models of dispersal. Because areas far apart in the Atlantic Forest usually have distinct climates, it is difficult to determine whether these areas have distinct species due to their geographical separation or differences in climatic conditions (Legendre *et al.*, 2005; de la Sancha *et al.*, 2014).

As in many other studies, similarity in composition of Atlantic Forest small-mammals decayed with geographic distance

Table 2 Simple and multiple Generalized Linear Models (GLM) comparing the association of species similarity against geographical distance and environmental dissimilarity. Geographical distance was the strongest predictor of the Jaccard similarity index both when analyzed in isolation or when combined with other variables. Similar results were found for the overall Jaccard similarity index and the turnover component of the Jaccard similarity index. $b_{sim}$: slope of individual predictor variables in simple GLMs; $P_{sim}$: $P$-values of individual predictor variables in simple GLMs; $b_{mult}$: slope of individual predictor variables in multiple GLMs; $P_{mult}$: $P$-values of individual predictor variables in multiple GLMs.

| Response variable | Explanatory variable | $b_{sim}$ | $P_{sim}$ | $b_{\mathrm{mult}}$ | $P_{\mathrm{mult}}$ |
|---|---|---|---|---|---|
| Jaccard similarity (turnover + nestedness) | Geographic distance | −0.293 | < 0.001 | −0.231 | 0.006 |
| | Climatic dissimilarity | −0.119 | < 0.001 | −0.033 | 0.158 |
| | Habitat dissimilarity | −0.013 | 0.359 | −0.015 | 0.355 |
| Jaccard similarity (turnover) | Geographic distance | −0.319 | < 0.001 | −0.207 | 0.01 |
| | Climatic dissimilarity | −0.124 | < 0.001 | −0.058 | 0.049 |
| | Habitat dissimilarity | 0.099 | 0.981 | 0.113 | 0.992 |

between grid cells (Fig. 4; Table 2). These distance-decay relationships are often interpreted as evidence for community assembly via dispersal limitation, or of spatially structured environmental effects (Nekola & White, 1999). Although the distance-decay relationship for small-mammals can be fit by a GLM ($r^2$ ~0.25; Fig. 4), the shape of the curve does not match the quantitative predictions of the neutral or spreading dye models, which both generated a steeper decay profile. The climatic model predicted a much shallower distance-decay relationship, and the habitat model predicted no decay with distance (Fig. 4). As Tuomisto & Ruokolainen (2006) have emphasized, the distance-decay relationship is not measuring the same thing as species composition calculated by ordination methods. When species composition is measured with the PCoA ordination, the fit is considerably improved for both the neutral and spreading dye models ($r^2 = 0.74, 0.73$, respectively; Table 1), but is weaker for the climatic and habitat models ($r^2 = 0.62, 0.11$, respectively; Table 1).

## Controversy of neutral and spreading dye modes

In our analyses, the neutral and spreading dye models generated predictions that were virtually identical for species richness and composition. This was not a surprise given that both models simulated the spreading of dispersal-limited species in a homogeneous bounded domain. Rangel & Diniz-Filho (2005) were the first to demonstrate that these models have qualitatively similar predictions for species richness. Our results indicate that these models also generate similar predictions for species composition. Despite the higher flexibility of the neutral model, in which species dispersal could range from highly limited to almost no limitation, the best fit of the neutral model for species composition was found with very limited dispersal, producing coherent species ranges as the mid-domain model.

In the last decade there has been a lot of debate about the validity and utility of neutral and mid-domain models in ecology (Colwell *et al.*, 2004; Currie & Kerr, 2008; Clark, 2012; Ricklefs, 2012). The main argument against neutral and mid-domain models is that other (non-neutral) processes can generate similar patterns of species distribution (Currie & Kerr, 2008; Rosindell *et al.*, 2012). When competing models generate similar predictions for a given metric, such as the neutral and spreading dye models, none of the models can be ruled out.

Despite the controversy, the neutral and mid-domain models continue to be popular because they are simple and parsimonious, and often have a strong predictive power, even when some assumptions are violated (Rosindell *et al.*, 2012). Moreover, these models can be easily extended for more realism (Rahbek *et al.*, 2007; Rosindell *et al.*, 2012).

Both the neutral and spreading dye models had similar predictions, and were better predictors of species composition than models based on individual species responses to climatic conditions and habitat quality. These results suggest that dispersal and geometrics constraints may contribute to variation in small mammal species composition across the Atlantic Forest. At smaller spatial scales, where dispersal limitation is not prominent, species adaptations to the environment are more likely to be important (Hurtt & Pacala, 1995). Because climate can limit species dispersal and establishment, it may be difficult to disentangle their separate effects.

In this study, local species richness ($\alpha$-diversity) was best explained by a model of habitat quality, whereas regional species composition ($\beta$-diversity) was best explained by neutral or spreading dye models or by correlations with climatic variables. These results suggest that local and regional species diversity might result from different processes. Studies investigating only richness or composition are likely to conclude that either species dispersal or association with the environment is more important. In fact, both processes might act simultaneously with contrasting effects on richness and composition.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

**Figure S1** Small-mammal species richness predicted by individual climatic variables.

**Figure S2** Small-mammal species composition predicted by individual climatic variables.

**Figure S3** Species richness predicted by logistic regressions of individual species and by linear regressions of species richness against the predictor variables.

**Figure S4** First principal coordinates axis of species composition predicted by logistic regressions of indivudual species and by linear regressions of species richness against the predictor variables.

**Figure S5** Second principal coordinates axis of species composition predicted by logistic regressions of indivudual species and by linear regressions of species richness against the predictor variables.

**Figure S6** Network representation used to simulate small-mammal dispersal in the Atlantic Forest.

**Table S1** List of studies surveyed for small-mammal data.

**Table S2** Fit of models for species richness and compositon correcting for species prevalence.

## BIOSKETCH

Cristian Dambros is interested in the effects of dispersal and species adaptations to the environment on macroecological patterns of species distribution. He has studied the macroecology of soil invertebrates, plants, and small mammals in tropical forests of Brazil. Visit http://www.uvm.edu/~cddambro for more details.

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