Cristian S. Dambros[1]

measure of habitat quality.

Habitat quality was the single best predictor of local species richness (α-diversity), but was a poor predictor of local species composition and of the decay in species similarity with distance (β-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.

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.

α-diversity, β-diversity, cellular automata, dispersal limitation, distance-decay, Generalized Linear Model, habitat loss, mid-domain effect.

*Correspondence: Cristian S. Dambros,
Department of Biology, University of Vermont.
109 Carrigan Drive 120A Marsh Life Science
Bld. Burlington, VT 05405, USA.
E-mail: csdambros@gmail.com;
cristian.dambros@uvm.edu

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;

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 distribu-

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 = hdinformation aaafrindio 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 individ n4(r)-10.4(i)0.32g10.4(i)08.3(o)2.5(r)11.7(e1.2r)-10ox12(lit)-13.2(y)-variablyinsaticregrassonsn.
the robabilit species occurrence estimat92.2(ee)-430.3f(r)45.3(me)-430.3logr satic
model, and y, the species prele(nc)122(he)-420.1(()05(R)2

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

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.

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).

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 ($b_{GLM} \leq |0.02|$; Table 2). Similar results were found when the turnover component in the Jaccard similarity index was separated from the nestedness component.

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

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).

[illegible]

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 demonstrateyeCon5e-t6t(O)12.1(e)-/s(17222.1(m)0.4bi40.7(anananananananan2tnan195(climati*la2tnanoi5(clane)2.7(r)r)12(edicti1376.)n

Baselga, A. (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, **21**, 1223–1232.

Byrd, R., Lu, P., Nocedal, J. & Zhu, C. (1995) A limited memory algorithm for bound constrained optimization. *SIAM Journal on Scientific Computing*, **16**, 1190–1208.

Carnaval, A.C. & Moritz, C. (2008) Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *Journal of Biogeography*, **35**, 1187–1201.

Carnaval, A.C., Waltari, E., Rodrigues, M.T., Rosauer, D., VanDerWal, J., Damasceno, R., Prates, I., Strangas, M., Spanos, Z., Rivera, D., Pie, M.R., Firkowski, C.R., Bornschein, M.R., Ribeiro, L.F. & Moritz, C. (2014) Prediction of phylogeographic endemism in an environmentally complex biome. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20141461.

Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.-J. (2006) Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics*, **62**, 361–371.

Chiarello, A.G. (1999) Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. *Biological Conservation*, **89**, 71–82.

Clark, J.S. (2012) The coherence problem with the Unified Neutral Theory of Biodiversity. *Trends in Ecology & Evolution*, **27**, 198–202.

Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2004) The mid-domain effect and species richness patterns:what have we learned so far? *The American Naturalist*, **163**, E1–23.

Costa, L.P., Leite, Y.L.R., Fonseca, G.A.B. & Fonseca, M.T. (2000) Biogeography of South American forest mammals: endemism and diversity in the atlantic forest. *Biotropica*, **32**, 872–881.

Currie, D.J. & Kerr, J.T. (2008) Tests of the mid-domain hypothesis: a review of the evidence. *Ecological Monographs*, **78**, 3–18.

Diamond, J.M. (1972) Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest pacific islands. *Proceedings of the National Academy of Sciences of the United States of America*, **69**, 3199–3203.

Diniz-Filho, J.A.F., Siqueira, T., Padial, A.A., Rangel, T.F., Landeiro, V.L. & Bini, L.M. (2012) Spatial autocorrelation analysis allows disentangling the balance between neutral and niche processes in metacommunities. *Oikos*, **121**, 201–210.

Dornelas, M. (2010) Disturbance and change in biodiversity. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 3719–3727.

Economo, E.P. & Keitt, T.H. (2008) Species diversity in neutral metacommunities: a network approach. *Ecology Letters*, **11**, 52–62.

Economo, E.P. & Keitt, T.H. (2010) Network isolation and local diversity in neutral metacommunities. *Oikos*, **119**, 1355–1363.

Eiten, G. (1983) *Classificação da vegetação do Brasil*. CNPq, Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brasília.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487–515.

Gotelli, N.J., Anderson, M.J., Arita, H.T. *et al.* (2009) Patterns and causes of species richness: a general simulation model for macroecology. *Ecology Letters*, **12**, 873–886.

Haffer, J. (1985) Avian zoogeography of the neotropical lowlands. *Ornithological Monographs*, **36**, 113–146.

Halley, J.M. & Iwasa, Y. (2011) Neutral theory as a predictor of avifaunal extinctions after habitat loss. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 2316–2321.

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

Hurlbert, S. (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, **52**, 577–586.

Hurtt, G.C. & Pacala, S.W. (1995) The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology*, **176**, 1–12.

Jetz, W. & Rahbek, C. (2001) Geometric constraints explain much of the species richness pattern in African birds. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 5661–5666.

Krasnov, B.R., Shenbrot, G.I., Mouillot, D., Khokhlova, I.S. & Poulin, R. (2005) Spatial variation in species diversity and composition of flea assemblages in small mammalian hosts: geographical distance or faunal similarity? *Journal of Biogeography*, **32**, 633–644.

Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Ockinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2009) Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology & Evolution*, **24**, 564–571.

Legendre, P., Borcard, D. & Peres-Neto, P.R. (2005) Analyzing beta diversity: partitioning the spatial variation of

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Stevens, M.H.H. & Wagner, H. (2008) Vegan: community ecology package.

Prevedello, J.A., Figueiredo, M.S.L., Grelle, C.E.V. & Vieira, M.V. (2013) Rethinking edge effects: the unaccounted role of geometric constraints. *Ecography*, **36**, 287–299.

R Development Core Team (2013) R: a language and environment for statistical computing.

Rahbek, C., Gotelli, N.J., Colwell, R.K., Entsminger, G.L., Rangel, T.F.L.V.B. & Graves, G.R. (2007) Predicting continental-scale patterns of bird species richness with spatially explicit models. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **274**, 165–174.

Rangel, T.F.L.V.B. & Diniz-Filho, J.a.F. (2005) Neutral community dynamics, the mid-domain effect and spatial patterns in species richness. *Ecology Letters*, **8**, 783–790.

Real, R., Barbosa, A.M. & Vargas, J.M. (2006) Obtaining Environmental Favourability Functions from Logistic Regression. *Environmental and Ecological Statistics*, **13**, 237–245.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J. & Hirota, M.M. (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, **142**, 1141–1153.

Ricklefs, R.E. (2012) Naturalists, natural history, and the nature of biological diversity. *The American Naturalist*, **179**, 423–435.

[redacted]