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Jayme A. Prevedello

Universidade de Sao Paulo - USP

Nicholas J. Gotelli

University of Vermont

Jean Paul Metzger

Universidade de Sao Paulo - USP

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A stochastic model for landscape patterns of biodiversity

JAYME A. PREVEDELLO,^{1,3} NICHOLAS J. GOTELLI,² AND JEAN PAUL METZGER¹

¹Departamento de Ecologia, Universidade de São Paulo, São Paulo 05508 900 Brazil

²Department of Biology, University of Vermont, Burlington, Vermont 05405 USA

Abstract. Many factors have been proposed to affect biodiversity patterns across landscapes, including patch area, patch isolation, edge distances, and matrix quality, but existing models emphasize only one or two of these factors at a time. Here we introduce a synthetic but simple individual-based model that generates realistic patterns of species richness and density as a function of landscape structure. In this model, we simulated the stochastic placement of home ranges in landscapes, thus combining features of existing random placement and mid-domain effect models. As such, the model allows investigation of whether and how geometric constraints on home range placement of individuals scale up to affect species abundance and richness in landscapes. The model encompassed a gradient of possible landscapes, from a strictly homogeneous landscape to an archipelago of discrete patches. The model incorporated only variation in home range size of individuals of different species, with a simple suitability index that controlled home range spread into areas of habitat and areas of inter-habitat matrix. Demographic details of birth, death, and migration, as well as effects of species interactions were not included. Nevertheless, this simple model generated realistic patterns of biodiversity, including species–area curves and increases in diversity and abundance with decreasing isolation and increasing distance from patch edges. Species–area slopes (z values) generated by the model fell within the range observed in empirical studies on both true islands and habitat patches. Isolation and edge effects were stronger when the matrix was unsuitable, and became progressively weaker as matrix suitability increased, again in accordance with many empirical studies. When applied to a real data set on the abundance of 20 small mammal species sampled in forest patches in the Atlantic Forest of Brazil, the model predicted increases in abundance and richness with increasing patch size, consistent with the general pattern observed with field data. The ability of this simple model to reproduce realistic qualitative patterns of biodiversity suggests that such patterns may be driven, at least in part, by geometric constraints acting on the placement of individual ranges, which ultimately affect biodiversity patterns at the landscape level.

Key words: edge effects; geometric constraints; habitat fragmentation; island biogeography; matrix; mid-domain effect; neutral theory; null model; random placement; species–area relationship.

INTRODUCTION

Spatial variation in species diversity across landscapes has intrigued ecologists for more than a century, and is now considered a central research subject in biogeography, macroecology, community ecology, and landscape ecology (Brown 1995, Forman 1995, Ewers and Didham 2006, Lomolino et al. 2006, Gotelli et al. 2009). Many primary drivers of spatial variation in diversity have been identified, four of which have received prominent attention: area, isolation, edge effects, and matrix suitability (Ewers and Didham 2006, Fig. 1A). The most studied of these effects are *area* and *isolation*, which are important determinants of species richness in islands, habitat patches, or sampling sites (MacArthur and Wilson 1967, Connor and McCoy 1979, Watling and Donnelly 2006, Triantis et al. 2012, Fahrig 2013). In heterogeneous

landscapes in which habitat patches are surrounded by matrix habitats (i.e., habitats less permeable and suitable for reproduction of the focal species compared to the original habitat; Villard and Metzger 2014), many studies have also revealed the existence of *edge effects*: variation in abundance and richness related to the proximity of habitat–matrix boundaries (Murcia 1995, Ries et al. 2004, Banks-Leite et al. 2010). Moreover, *matrix suitability*, or the contrast between the habitat patch and the matrix, also affects population abundance and community richness within habitat patches and thus can mediate or interact with area, isolation, and edge effects (Fig. 1A; MacArthur and Wilson 1967, Ricketts 2001, Prevedello and Vieira 2010, Driscoll et al. 2013). Although the overall influences of area, isolation, edge effects, and matrix suitability on species abundance and richness are well established (Fig. 1A), there is still much debate on the specific causal mechanisms linking such factors to patterns of species richness and abundance (Ries et al. 2004, Ewers and Didham 2006, Driscoll et al. 2013).

Four major classes of models have been used to investigate diversity patterns across landscapes (Fig. 1B). These

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Corresponding Editor: B. J. Cardinale.

³Present address: Departamento de Ecologia, Universidade do Estado do Rio de Janeiro, Rio de Janeiro 20550013 Brazil.
E-mail: ja_prevedello@yahoo.com.br

models can be categorized as dynamic vs. static models in patchy vs. continuous landscapes. The MacArthur and Wilson (1967) equilibrium model of island biogeography is an example of a model that is dynamic in a patchy (insular) landscape. According to this model, the number of species on an island results from a dynamic balance between species immigration and extinction, their ratio being higher for larger and less isolated islands (MacArthur and Wilson 1967). The idea that the number of species reflects a dynamic balance between extinction and immigration greatly influenced ecology and conservation biology (review in Losos and Ricklefs 2010). However, the same idea also proved to be one of the most controversial features of the equilibrium model, with many studies questioning the importance of species extinction and turnover in landscapes (Simberloff 1976, Gilbert 1980, Coleman et al. 1982, Schoener 2010). This cell (Fig. 1B) may also include many formulations of recent metacommunity models (Leibold et al. 2004), which have extended the original MacArthur-Wilson (1967) model by incorporating species interactions and migration among patches.

An example of a dynamic model in a continuous landscape is the original version of the neutral model (Fig. 1B; Hubbell 2001). In contrast to the equilibrium model, the neutral model is an individual-based rather than a species-based model that simulates the stochastic birth, death, and migration of individuals (Hubbell 2001). Another important distinction between these two models is that the original neutral model (Hubbell 2001) focused on homogeneous landscapes, whereas the equilibrium model focused on patchy landscapes (Fig. 1B). More recently, the neutral model has been extended to more spatially explicit versions applicable to patchy landscapes, in which habitat patches are embedded within a matrix of lower habitat quality (Campos et al. 2012, Teyssèdre and Robert 2014).

In contrast to these dynamic models, a different class of models has shown that gradients in biodiversity may occur even when extinction processes or species turnover are not explicitly incorporated (Fig. 1B). Such “static” models include the random placement model (Coleman 1981, Coleman et al. 1982) and the mid-domain effect model (Colwell and Lees 2000). The random placement model was developed as a potential statistical explanation for the species–area relationship represented as a pure island system (Coleman 1981). According to this model, habitat patches function as “targets” that accumulate individuals passively. Large patches accumulate more individuals and, consequently, more species than small patches. Because it is based on probabilistic processes, and does not include any explicit ecological mechanism, the random placement model has been used as a null model for comparing with real data and with the predictions of more complex models (Coleman et al. 1982, Gotelli and Graves 1996, Bidwell et al. 2014). The mid-domain effect model simulates the stochastic origin and spread of species’ geographical ranges, and has traditionally been used to investigate variation in species richness at much larger spatial scales

(whole continents and large elevational gradients), and across contiguous rather than patchy landscapes (Fig. 1B; Colwell and Lees 2000, Gotelli et al. 2009). Recently, mid-domain models have also been used to investigate edge effects at the scale of habitat patches (Prevedello et al. 2013, see also Tiwari et al. 2005). The main contribution of mid-domain models was to show that geometric constraints, acting on the placement of species’ geographical ranges (Colwell and Lees 2000) or individual home ranges (Prevedello et al. 2013), can produce gradients in species richness or abundance even when historical processes or effects of contemporary climate or habitat quality are not explicitly incorporated (Colwell et al. 2004, Tiwari et al. 2005, Gotelli et al. 2009, Prevedello et al. 2013). Like the random placement model, the mid-domain effect model has been adopted as a null or baseline model (Gotelli and Graves 1996, Colwell et al. 2004, Prevedello et al. 2013).

Despite the major conceptual contribution of these four types of models to the study of biodiversity patterns across landscapes, their potential use has been limited for three reasons. First, each of these models focuses on an extreme landscape pattern, in which the matrix is either completely suitable or completely unsuitable to individuals (Fig. 1B). Such landscapes are better viewed as the two end points in a continuum of landscapes with varying degrees of matrix suitability. Indeed, in most terrestrial landscapes, the matrix is neither completely hospitable nor completely inhospitable to individuals, but instead serves as a secondary habitat for many species (Gascon et al. 1999, Prevedello and Vieira 2010, Driscoll et al. 2013). A second limitation of these models is that they ignore variation in animal body size, which is ubiquitous in nature (Peters 1983) and is known to influence species responses to habitat area and isolation (Henle et al. 2004, Ewers and Didham 2006, Vetter et al. 2011). Body size determines individuals’ metabolic rates (Brown et al. 2004), which in turn affects many individual and population characteristics, including home range size and population abundance (Damuth 1981, Peters 1983, Kelt and Van Vuren 2001, Brown et al. 2004). Home range size, in particular, has been suggested as an important determinant of species responses to habitat area and isolation (Börger et al. 2008, Buchmann et al. 2011). Third, the classic models ignore much of the variation in the spatial configuration of habitat in landscapes, such as the specific location and the shape of habitat patches. The spatial configuration of habitat may regulate the occurrence and intensity of geometric constraints, which in turn may affect home range placement, with potentially pervasive impacts on species’ occurrence and abundance across the landscape. Geometric constraints acting on home range placement have been shown recently to occur at the scale of individual habitat patches, reducing the abundance of organisms near patch boundaries (Prevedello et al. 2013). However, the implications of geometric constraints for the distribution of individuals at the landscape level, and therefore for community richness and abundance, have not been explicitly investigated yet. Due to these limitations, each of

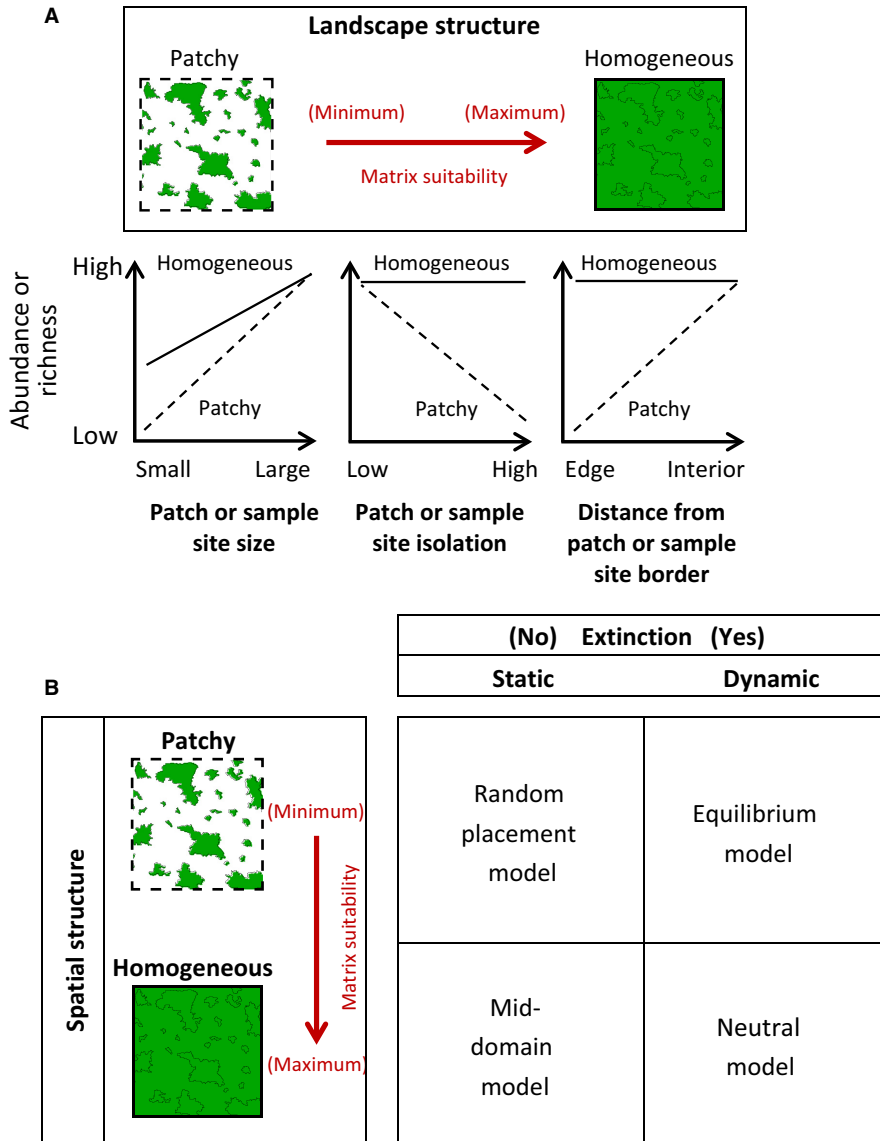


FIG. 1. (A) Well-supported generalizations on the influence of area, isolation, edge, and matrix effects on abundance and species richness (modified from Ewers and Didham 2006). The spatial structure of landscapes can range from patchy to homogeneous, according to matrix suitability. In the first case, habitat patches can be clearly defined, whereas in the second no patches exist, only sample sites with boundaries arbitrarily defined. Although a “landscape” is often described as a “spatially heterogeneous area” (Turner 1989), here we treat a “homogeneous landscape” as an extreme spatial pattern, one of the endpoints of a gradient of relative matrix suitability in which matrix and habitat are indistinguishable. The matrix can also mediate area, isolation, and edge effects. General patterns of increase or decrease are depicted as linear relationships to simplify, but in reality may take nonlinear forms (e.g., exponential, power law). (B) Representation of the main theoretical models used in the study of area, isolation, edge, and matrix effects according to the type of landscapes considered (patchy or homogeneous) and the inclusion vs. the exclusion of extinction processes (dynamic or static, respectively).

previous models allow investigation of only one or two of the four main drivers of spatial variation in diversity, but not all drivers simultaneously.

Here we show that a simple modification of the random placement model that incorporates body size and explicitly considers matrix suitability is able to reproduce realistic gradients of spatial variation in species diversity from homogeneous to patchy landscapes. This model, hereafter called the

landscape model, explicitly simulates the stochastic placement of home ranges in landscapes. It is analogous to mid-domain effect models used in macroecology, which simulate the placement of species’ geographical ranges across biogeographical scales (Gotelli et al. 2009). As such, the landscape model reveals whether and how geometric constraints, acting on home range placement, affect biodiversity patterns in landscapes. The model combines elements of two

TABLE 1. Parameters used to construct the landscapes and mammal assemblages used in the simulations and sources used to support their choices.

Parameter	Value	Explanation	Source
Landscape construction			
Landscape size	300×300	dimensions of the landscape (n cells)	Jackson and Fahrig (2014)
Habitat cover	0.10, 0.30	proportion of the landscape occupied by habitat	Villard and Metzger (2014)
Habitat aggregation	0.55	probability of aggregation of habitat cells	Saura and Martínez-Millán (2000)
Matrix suitability	0, 0.4, 0.8, 1.0	probability of occupancy of matrix cells by individuals	Driscoll et al. (2013)
Assemblage construction			
Total species richness	100	number of species in the assemblage	Buchmann et al. (2011)
Body size limits	0.1, 100	minimum and maximum body mass (kg)	Buchmann et al. (2011)
Body size distribution	$p(M) = k \times M^n$	function to attribute a body mass (M) to each species; k is a constant	Buchmann et al. (2011)
Body mass exponent	-0.77, -1.10, -1.31	exponent of the previous function (n)	Buchmann et al. (2011)
Density	$\log D = 1.21 - 0.7 (\log M)$	function to calculate density (D) from body mass	Silva and Downing (1995)
Home range size	$\log HR = -2.33 + 1.13 (\log M)$	function to calculate home range (HR) from body mass	Kelt and Van Vuren (2001)

previous null models, the random placement model and the mid-domain effect model, which have been so far considered rather separately in the literature. We first explored the behavior of the landscape model using simulated mammal communities and landscapes. We explored the parameter space of this model and evaluated how the distribution of body sizes among species and the suitability of the matrix affected model outcomes. In addition, we analyzed a real data set on small mammal assemblages to illustrate how the model can be used in empirical applications. We show that the landscape model is able to reproduce empirically observed area, isolation, edge, and matrix effects on communities (as summarized in Fig. 1A), even when species interactions, extinction, and other demographic processes are not explicitly incorporated.

METHODS

Overview

The landscape model simulates the stochastic origin and spread of individual home ranges across a gridded landscape analogously to traditional mid-domain effect models, which simulate the distribution of geographic ranges of species across larger continental scales (Colwell et al. 2004). To explore the behavior of the landscape model, we performed simulations using realistic parameter estimates for biological communities and landscapes (Table 1). Each species in the simulated community had a particular body mass derived from an input power-law distribution, which was used to estimate its population density and home range size based on well-established allometric functions. Simulations were run using increasing values for the suitability of the matrix, which

generated a spectrum of artificial landscapes ranging from strictly patchy to purely homogeneous.

Landscape construction

Landscapes were created using the modified random cluster method (Saura and Martínez-Millán 2000), which provides independent parameters controlling the percentage and degree of aggregation of suitable habitat in the landscape. Each landscape was represented as a grid of 300×300 cells. Each cell represented an area of 50×50 m, thus the landscape encompassed 225 km^2 or $22,500 \text{ ha}$, large enough for a robust investigation of the main patterns of biodiversity distribution across landscapes (Fig. 1A; see Jackson and Fahrig 2014). Each grid cell was classified as either habitat or matrix. The proportion of habitat cells in the landscape was set to either 10% or 30% of the total area of the landscape, based on previous studies that suggested that the effects of patch size and isolation should be more pronounced around those proportions (Andrén 1994, Pardini et al. 2010, Villard and Metzger 2014). The degree of aggregation of habitat cells was controlled by the parameter p , with $p = 0$ resulting in a completely random distribution and $p \approx 0.593$ resulting in a completely clumped distribution (see Saura and Martínez-Millán 2000). We set p to a high, but not extreme, value ($p = 0.55$), which results in realistic landscapes (Saura and Martínez-Millán 2000). For comparison, in Appendix S1 we present model outcomes for a landscape with a very low degree of aggregation of habitat cells ($p = 0.10$). Although similar general patterns emerge in landscapes with low and high habitat aggregation, there are quantitative differences in the predictions, illustrating that the landscape model is sensitive to habitat configuration (see Appendix S1).

For each percentage of cover, we generated 30 replicate landscapes. We present in detail in the main text only the results for one landscape with 30% of habitat cover, and overall results for the different replicates of landscapes with 30% of habitat cover (see *Data analysis*), because the model reproduced the same general patterns for the landscape with 10% habitat cover (Appendix S2). Patch sizes in the landscape that is illustrated in the main text ranged from 1 (0.25 ha) to 3964 grid cells (991 ha), thus spanning ~ 3.6 orders of magnitude, which encompasses the range of patch sizes used in most studies on patchy landscapes (mean \pm SD = 2.75 ± 0.08 orders of magnitude; Watling and Donnelly 2006). Landscapes were created using the package *seccr* 2.6.0 (Efford 2013) in the R 3.2 environment (R Core Team 2014).

To evaluate how matrix suitability affected model outcomes, we varied it from the extreme values of 0 (completely inhospitable matrix) to 1 (as hospitable as the habitat patches). Here, matrix is defined simply as the landscape cells that were not set as habitat cells during the creation of the simulated, binary landscapes. In the case of a completely inhospitable matrix, individuals could not establish their home ranges in the matrix, as is the case in oceanic island systems, and as assumed in the random placement model and in the classic equilibrium model of island biogeography (Fig. 1B). In the case of a hospitable matrix, matrix and habitat patches were indistinguishable and the landscape was homogenous, without any habitat fragmentation, similar to classic mid-domain effect and neutral models (Fig. 1B). In this scenario, the areas within which abundance and richness are measured are not habitat patches but simply sampling areas, with the same shape, size, and location as the habitat patches that occur in the same landscape when matrix suitability is lower than habitat suitability. We also explored intermediate values of matrix suitability (0.4 and 0.8), representative of many patchy terrestrial landscapes, in which individuals can use the matrix as a secondary habitat (Prevedello and Vieira 2010, Driscoll et al. 2013).

Assemblage construction

We constructed mammal assemblages of 100 species each, which encompasses the range of species richness found in most local assemblages of mammals (see Buchmann et al. 2011). Each species in the assemblage was assigned a particular home range size and population abundance, estimated from its body mass. Body mass was used only as an indirect proxy to estimate abundance and home range for each species in the different communities simulated. We used mammals as model organisms with species' body masses ranging from 0.1 to 100 kg, because the relationships between body mass and home range size and population density are well known for this group and for this range of body mass (Silva and Downing 1995, Kelt and Van Vuren 2001). However, the model may be applied for any animal group for which home range size

and population density estimates are directly available or can be estimated from body mass.

To attribute a particular body mass (M) to each species in the simulated communities, we used a power-law distribution based on Buchmann et al. (2011), $p(M) = k \times M^n$, where k is a constant chosen so that the equation integrates to 1. The exponent of the relationship (n) determines how uniform the distribution of body masses among species is. We constructed communities using three realistic n values, -1.31 (more uneven distribution of body masses), -1.10 (intermediate), and -0.77 (more uniform distribution), which correspond to the maximum, intermediate, and minimum values measured for real mammal communities (Buchmann et al. 2011). In the main text, we present only the results for communities with intermediate n values (-1.10), because the results were similar for the other communities (see Appendix S3).

Based on the body mass of each species, we calculated its total population density (D) as $\log(D) = 1.21 - 0.7(\log M)$, following Silva and Downing (1995). Based on the calculated density (expressed as number of individuals/km²) and the total area of the landscape (225 km²), we determined how many individuals of the species would be placed in the landscape. Model outputs were similar when the number of individuals to be placed in the landscape was calculated in proportion to matrix suitability (Appendix S4). The home range (HR) of each species was also estimated as a function of body mass, following Kelt and Van Vuren (2001): $\log(\text{HR}) = -2.33 + 1.13(\log M)$.

Home range placement in the landscape

The landscape model simulates the stochastic origin and spread of individual home ranges within a gridded landscape. For each individual, a grid cell is randomly chosen to represent the birth of the individual. The probability that a given cell is chosen as the birth cell is proportional to its suitability, which is set as 1 for all habitat cells and between 0 and 1 for matrix cells. When matrix suitability = 0, however, the suitability of habitat cells belonging to patches that are smaller than the home range is also set to 0, because the patch would be too small to contain even a single home range. Each individual then expands its home range by occupying adjacent cells, until the final home range size (as determined from the species' body mass) is reached. Home range expansion follows a modified "spreading dye" algorithm (Jetz and Rahbek 2001), used in more recent mid-domain effect models that incorporate habitat variation (Storch et al. 2006, Rahbek et al. 2007). In this algorithm, the second, third, ..., n th cells are chosen with a probability proportional to their suitability, but only the eight adjacent contiguous cells (Moore neighborhood) are considered as candidate cells. This restriction ensures the cohesion of home ranges while allowing for realistic variation in their shape (Prevedello et al. 2013). The model was implemented in R 3.2 (R Core Team 2014). The full code used to construct the

communities and landscapes, and to place home ranges in the landscape, is provided in the Supplement 1.

The landscape model assumes the absence of territorial behavior, in the sense that individuals of a same species are placed independently in the landscape. To explore the consequences of relaxing this assumption, we also ran the landscape model considering the extreme case of strict territorial behavior, in which the home ranges of individuals of the same species were not allowed to overlap (Appendix S5). Results were robust to the incorporation of territorial behavior: the qualitative patterns of abundance and richness among patches and cells were maintained, despite quantitative differences in the results (Appendix S5).

The landscape model also assumes that individuals do not disperse, in the sense that they always settle their home ranges in the vicinities of the birth cell. To evaluate the sensitivity of the model to this assumption, we tested two alternative versions that incorporated simple dispersal, as detailed in the Appendix S6. The outcomes of these models were almost identical, and in general they were also similar to those of the model without dispersal. The only important difference was the emergence of mid-domain effects at the landscape scale in models that incorporated dispersal. Such mid-domain effects emerged because dispersing individuals tended to concentrate more near the center of the landscape (see Appendix S6: Fig. S1).

Data analysis

To investigate area, isolation, edge, and matrix effects on communities, we recorded total community abundance and richness per grid cell and per habitat patch. We then determined how matrix suitability modulated area, isolation, and edge effects, graphically comparing patterns generated by the landscape model with the expected patterns obtained from empirical studies in real landscapes (Fig. 1A). For the graphical analyses, raw abundance and richness per cell and per habitat patch were converted to relative values, calculated separately for each landscape as: (predicted value)/(maximum predicted value). With this transformation, abundance and richness always ranged from 0 to 1, facilitating comparisons of patterns between these two variables and also across landscapes with different matrix suitability.

In addition to the graphical analysis, we extracted the slopes of the species–area relationships (z values) from the logarithmic form of the power model ($S = cA^z$; Arrhenius 1921). We also calculated the expected species richness (± 2 SD), abundance, and density (abundance divided by patch size) for each patch as predicted by the random placement model, following Coleman (1981), and compared them with the values predicted by the landscape model.

Isolation was evaluated at the grid cell level using a modified version of the similarity index, which provides a biologically meaningful measure of effective isolation

(McGarigal et al. 2002). This index measures the similarity of the neighborhood of a given focal cell. Because the area of each cell was always the same, we calculated the index as the sum of the suitability of each cell within a search buffer that surrounded the focal cell divided by the square of its distance from the focal cell (McGarigal et al. 2002). The radius of the search buffer was calculated as the average median home range size of all species in the community, measured in number of cells, because home ranges can assume linear shapes and their size determines the potential of an individual reaching a given landscape cell in the model.

The similarity index was calculated for all cells in the landscape, including both habitat and matrix cells. Because the similarity index is negatively related to isolation (McGarigal et al. 2002), we converted it to a direct metric of isolation for each cell, by calculating the difference between the maximum similarity possible for a landscape cell and the observed similarity of the focal cell. Maximum similarity corresponded to the similarity of a cell completely surrounded by habitat cells within the search buffer. For both matrix and habitat cells, isolation effects were analyzed primarily at the cell rather than the patch level following the suggestions of Fahrig (2013). Isolation effects at the patch level are presented in Appendix S7 for comparison.

Edge effects were quantified by relating the abundance and species richness recorded at each habitat cell to the average distance from the patch edge, based on the eight compass directions of the Moore neighborhood.

Values shown in the figures of the main text were recorded after only a single run of the model. To check the consistency of such model outcomes across different iterations, we ran the landscape model 30 times, each one with a different community and a different landscape. These communities and landscapes differed because the model is stochastic, but they were constructed using the same parameter values (habitat amount in the landscape = 30%, aggregation of habitat patches [p] = 0.55, exponent of the power law distribution of body mass = -1.10). To summarize model outcomes for each iteration, we calculated the slopes of the following relationships (using log-transformed values to linearize relationships when necessary): (1) abundance vs. patch size; (2) log(density) vs. log(patch size); (3) log(species richness) vs. log(patch size); (4) abundance vs. pixel isolation; (5) richness vs. pixel isolation; (6) log(abundance) vs. log(distance from edge); (7) log(richness) vs. log(distance from edge).

Case study

To illustrate how the model can be fit to empirical data, we analyzed a data set on small mammal assemblages sampled at 20 forest sites in the Brazilian Atlantic Forest (Pardini et al. 2010). This data set has been analyzed in previous studies on the effects of habitat loss and fragmentation (Pardini et al. 2005, 2010, Banks-Leite et al. 2014, Püttker et al. 2015). It is particularly suitable to

illustrate the application of our model for a number of reasons. First, a previous analysis detected consistent patch-area effects on both abundance and species richness (Pardini et al. 2010) and another study carried out in the same landscape has shown the importance of incorporating matrix suitability to predict small mammal distribution across habitat patches (Umetsu et al. 2008). Second, the system is representative of many terrestrial, fragmented landscapes (Driscoll et al. 2013), with fragmented native habitats (forests) embedded in a matrix of different human-modified habitats. Third, the habitat preferences and home range sizes of the 20 small mammal species recorded in this landscape are relatively well known (Appendix S8). Finally, a large and standardized sampling effort was employed across the 20 forest sites, resulting in robust and directly comparable estimates of species abundance and richness.

The studied landscape is located in São Paulo state, Brazil (23°41'–23°46' S, 47°03'–47°07' W), within the domain of the Atlantic Forest biodiversity hotspot. The landscape is approximately 10000 ha, 31% of which is covered by native forest (see Fig. 9). The dominant habitat types surrounding native forest patches are plantations of annual crops (38% of the landscape), rural areas with buildings such as houses, greenhouses, and storage units (14%), native vegetation in initial stages of regeneration (7%), and homogeneous eucalyptus plantations (7%; see Fig. 9 and Umetsu and Pardini 2007 for details).

The 20 sampling sites were separated by at least 284 m (distance to the nearest surveyed site = $1,024 \pm 700$ m

[mean \pm SD]), and located within forest patches that were 2–374 ha in area. During the summers of 2001–2002 and 2002–2003, each of the 20 forest sites was surveyed with a 100-m array of 11 large pitfall traps, for a total of 32 trapping days (details in Pardini et al. 2010). Large pitfall traps deployed during the wet season each year yielded a large number of individuals and species, including rare species (Pardini et al. 2010).

To analyze patterns in community abundance and richness, we designated the 20 detected mammal species in two groups, “generalists” and “specialists,” following the original classification of Pardini et al. (2010). Specialist species were those whose geographical distribution is restricted to forested biomes (Atlantic Forest and Amazon) and are usually sensitive to the conversion of native forest into anthropogenic habitats. Generalist species were those whose geographical distribution also encompasses the non-forested biomes adjacent to the Atlantic forest (Cerrado and Caatinga; Pardini et al. 2010). For each species, we compiled from the literature empirical estimates of home range sizes and abundances in the different land-cover types (Table 2), as detailed in the Appendix S8.

For simulations, the landscape map was converted to a raster file containing 397×291 cells with cell size of 30 m, matching the extent and resolution of the original map. We fit the model to the data of each of the two sampling periods separately, and then averaged abundance and richness values across the two periods for analysis. Each species and individual was placed in the model landscape independently using the model

TABLE 2. Parameter estimates for the empirical case study on small mammals of the Atlantic Forest, Brazil.

Species	Land cover suitability					Home range (ha)	Total abundance
	For	Ini	Euc	Rur	Agr		
Specialist species							
<i>Marmosops incanus</i>	1.00	0.13	0.00	0.00	0.00	1.4	2464
<i>Brucepattersonius soricinus</i>	1.00	0.50	0.00	0.00	0.50	0.2	1323
<i>Monodelphis scalops/M. americana</i>	1.00	0.00	0.00	0.00	0.00	0.6	698
<i>Delomys sublineatus</i>	1.00	0.50	0.00	0.00	0.00	0.5	1475
<i>Sooretamys angouya</i>	0.75	1.00	0.00	0.00	0.00	2.2	1616
<i>Thaptomys nigrita</i>	1.00	0.50	0.00	0.00	0.50	0.1	70
<i>Gracilinanus microtarsus</i>	1.00	0.00	0.30	0.00	0.00	1.0	430
<i>Juliomys pictipes/J. ossitenuis</i>	1.00	0.50	0.00	0.00	0.10	1.0	67
<i>Euryoryzomys russatus</i>	1.00	0.00	0.00	0.00	0.00	1.6	148
<i>Monodelphis sorex (=M. dimidiata)</i>	1.00	0.00	0.50	0.00	0.50	0.6	50
<i>Phyllomys nigripinus</i>	1.00	0.00	0.00	0.00	0.00	2.4	81
<i>Oxymycterus dasytrichus</i>	1.00	0.00	0.00	0.00	0.00	1.6	167
<i>Rhagomys rufescens</i>	1.00	0.00	0.00	0.00	0.00	1.0	13
Generalist species							
<i>Akodon montensis</i>	0.08	1.00	0.39	0.10	0.05	1.0	6774
<i>Oligoryzomys nigripes</i>	0.04	0.60	1.00	0.08	0.20	0.6	32523
<i>Calomys tener</i>	0.10	0.10	0.00	0.27	1.00	0.2	942
<i>Necomys lasiurus</i>	0.10	0.10	0.00	0.50	1.00	0.9	190
<i>Nectomys squamipes</i>	1.00	1.00	0.00	0.00	0.00	2.8	9
<i>Bibimys labiosus</i>	0.10	0.10	0.10	0.10	1.00	0.2	269
<i>Lutreolina crassicaudata</i>	1.00	1.00	1.00	1.00	1.00	3.6	46

Notes: Land cover suitability varied from 0 (unsuitable for the species) to 1 (maximum suitability). For, native forest; Ini, native vegetation in initial stages of regeneration; Euc, Eucalyptus plantations; Rur, rural areas with buildings; Agr, areas of agriculture. Total abundance is the estimated total number of individuals in the entire landscape.

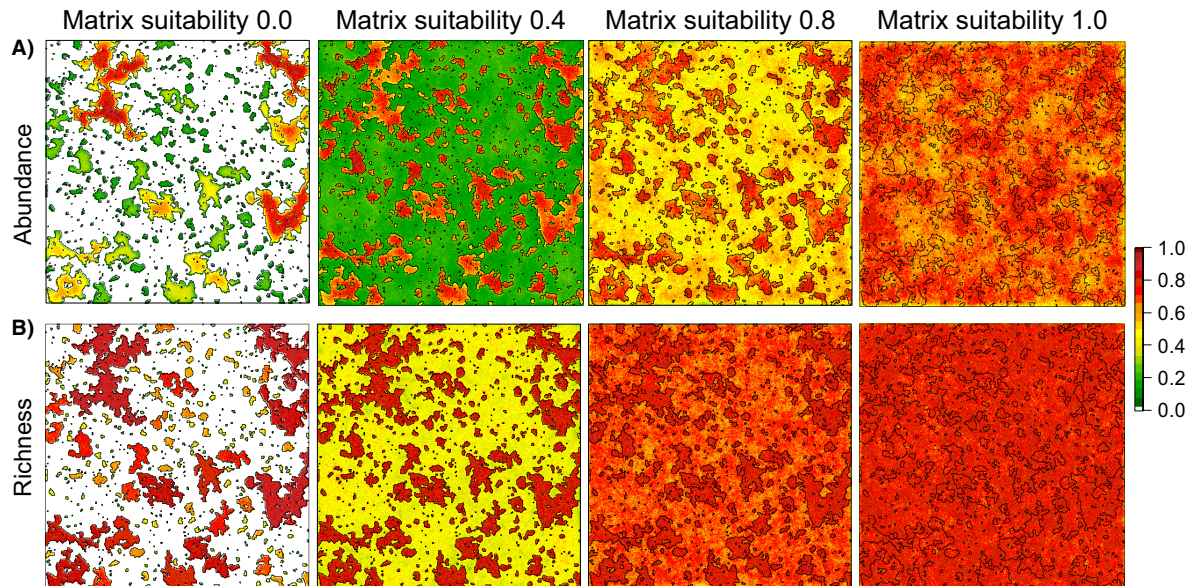


FIG. 2. General outputs of the landscape model for different matrix suitability values. Predicted abundance (A) and species richness per grid cell are shown as proportional values, calculated separately for each matrix suitability value as (predicted value)/(maximum (B) predicted value).

algorithms, assuming absence of strict territoriality, which is unlikely to occur in most of these species (Reis et al. 2011, Prevedello et al. 2013). We ran 100 iterations of the model for data of each sampling period, recording for each iteration the abundance and occurrence (presence/absence) of each species in each landscape cell.

We also fit Coleman's (1981) random placement model for comparison. To incorporate the assumptions of the Coleman model, we set the following parameters for all species: home range size = 1 cell, forest suitability = 1, and the suitability of all matrix types = 0. After 100 iterations, we recorded the total abundance and richness for each landscape cell, separately for specialist and generalist species.

For both abundance and species richness, we calculated the Pearson's coefficient of determination (r^2) between the observed value in each forest site and the average of the model prediction from 100 iterations. In addition, we tested whether the intercept differed significantly from 0, and whether the slope differed significantly from 1. If the data are perfectly predicted by the model, a regression of observed vs. predicted values will yield $r^2 = 1.00$, slope = 1.00, and intercept = 0.00. To analyze patch-area effects, we also correlated observed and predicted abundances and richness with $\log(\text{forest patch size})$, as in the original study of Pardini et al. (2010).

RESULTS

Matrix effects on general model outcomes

For both abundance and species richness, differences within and among habitat patches were more

pronounced when the matrix was completely unsuitable to individuals (Fig. 2). In this case, larger patches accumulated substantially more individuals and species than did smaller patches. In addition, abundance was visibly higher at the center of the patches compared to their edges, yielding a mid-domain effect at the scale of individual patches, which was less clear for species richness. As matrix suitability increased, differences within and among patches became progressively less conspicuous, disappearing when the landscape was homogenous (Fig. 2). In this case, there was no consistent difference in abundance or richness between habitat and matrix pixels, despite some random variation among pixels reflecting the stochastic nature of the model.

Area effects

Abundance always increased with the size of the habitat patch (or sample area in the case of the homogeneous landscape), but this relationship departed from the linear (1:1) relationship predicted by the random placement model for all but the largest patches (>2,000 cells). The deviation from predictions of the classic random placement model was especially evident in patches with fewer than 100 cells (Fig. 3A). Abundance in these smaller patches was slightly lower than predicted by the random placement model when the matrix was unsuitable, but higher than predicted in all other cases (Fig. 3A). Slopes of the abundance-area relationships decreased as matrix suitability increased (slopes = 25.35, 13.68, 9.74, and 8.61, for matrix suitability = 0, 0.4, 0.8, and 1.0, respectively).

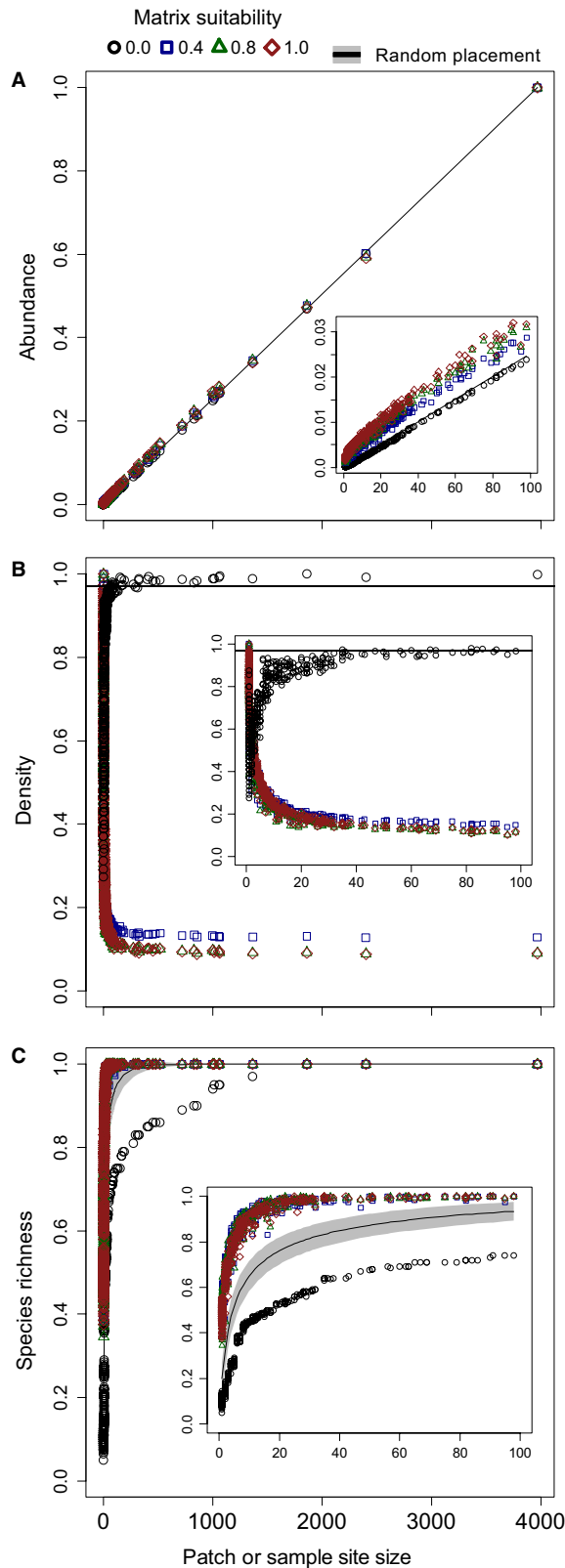


FIG. 3. Area effects on (A) abundance, (B) density, and (C) species richness for different matrix suitability values, as predicted by the landscape model. Predicted abundance, density, and species richness are shown as proportional values, calculated separately for each matrix suitability value as (predicted value)/(maximum predicted value). Insets highlight the results for the smallest patches or sample sites (<100 grid cells). Continuous lines indicate predictions (mean + 2 SD) of the random placement model.

Population density varied with the size of the patch (or sample area) in all degrees of matrix suitability (Fig. 3B). This is in contrast to the underlying assumption of the random placement model, which is a constant density for all patch sizes or sample areas. The density–area relationship was positive when the matrix was completely unsuitable, but negative in all other cases (Fig. 3B).

Species richness also increased with the size of the habitat patch (or sample area; Fig. 3C). Very large patches ($\geq 2,000$ grid cells) always contained all species (100 species), regardless of the degree of matrix suitability. On the other hand, variation in matrix suitability affected the number of species in patches with fewer than 2000 cells: they had fewer species than predicted by the random placement model when the matrix was completely unsuitable, but otherwise had more species than predicted (Fig. 3C). Slopes of the species–area relationships decreased as matrix suitability increased from 0 to 0.4 ($z = 0.40$ and 0.13 , respectively), and remained low for greater increases in matrix suitability ($z = 0.14$ for matrix suitability = 0.8 or 1.0).

Isolation effects

Abundance and richness within habitat cells generally decreased as cell effective isolation increased (Fig. 4B, C). This relationship was steeper when the matrix was unsuitable, and became progressively shallower as matrix suitability increased to 1. For matrix cells, richness and abundance were obviously 0 when matrix suitability was 0. In all other cases, abundance and richness were negatively related to effective isolation, and this relationship again became shallower as the matrix suitability increased. Matrix and habitat grid cells became progressively more similar in abundance and richness as the matrix suitability increased (Fig. 4B, C).

Edge effects

When the matrix was unsuitable, abundance and richness increased as the distance from the surrounding edges increased (Fig. 5). This relationship was more linear for abundance, but, for richness, the maximum values were constrained to 100 species. For both richness and abundance, the relationship became shallower as the matrix suitability increased and disappeared when the matrix was completely suitable.

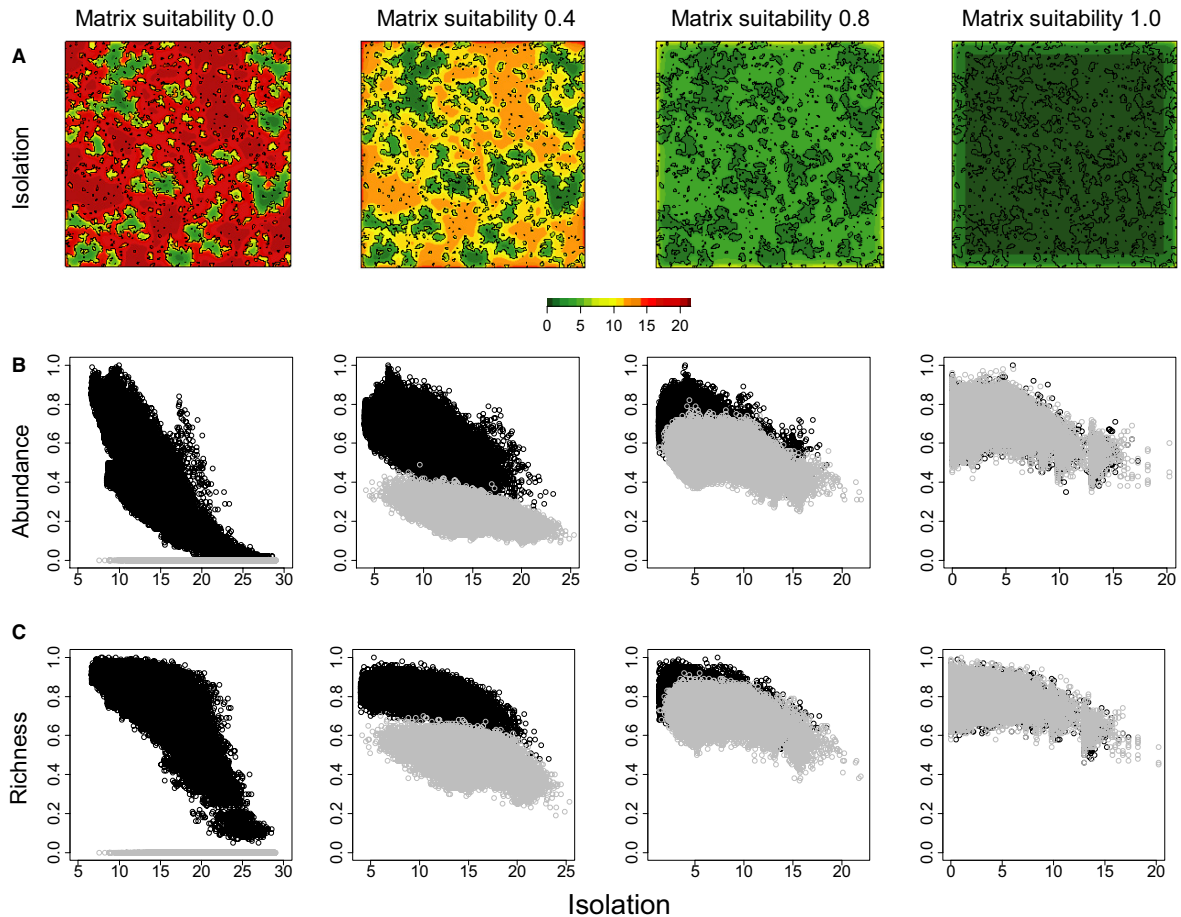


FIG. 4. Isolation effects. (A) Distribution of cell isolation values across the landscape for different matrix suitability values. Isolation was quantified as the complement of the similarity index (maximum similarity – observed similarity), using a search buffer of 18 cells (900 m). Higher values indicate higher effective isolations. (B) Isolation effects on abundance per grid cell, as predicted by the landscape model. (C) Isolation effects on species richness per grid cell, as predicted by the landscape model. Abundance and species richness are shown as proportional values, calculated separately for each matrix suitability value as (predicted value)/(maximum predicted value). Within each panel of B and C, habitat cells are shown in black and matrix cells in gray.

Consistency of model outcomes across different iterations

Across the 30 iterations of the model, slopes of the abundance–area relationships were always positive, and decreased as matrix suitability increased (Fig. 6A). Slopes of the density–area relationships were always positive when the matrix was completely unsuitable, but negative (reaching similar values) in all other cases (Fig. 6B). Slopes of the species–area relationships were always positive, and consistently higher when the matrix was completely unsuitable, reaching similarly lower values when matrix suitability was ≥ 0.4 (Fig. 6C).

For habitat cells, slopes of the abundance–isolation and richness–isolation relationships were always negative, and consistently higher (more negative) when the matrix was unsuitable, reaching similarly lower values when matrix suitability was ≥ 0.4 (Fig. 7). For matrix

cells, richness and abundance were obviously 0 when matrix suitability was 0. In all other cases, slopes of the abundance–isolation and richness–isolation relationships were always negative, with similar values for different matrix suitability values (Fig. 7).

Slopes of the relationships between abundance or richness with the distance from the surrounding edges were higher and positive when the matrix was completely unsuitable (Fig. 8). Slopes decreased as matrix suitability increased, reaching 0 when the matrix was completely suitable (Fig. 8).

Case study

For specialist small mammal species, observed abundance and richness increased significantly with patch size (abundance $r^2 = 0.59$, $P < 0.001$; richness $r^2 = 0.44$, $P = 0.001$). Similarly, the landscape model predicted

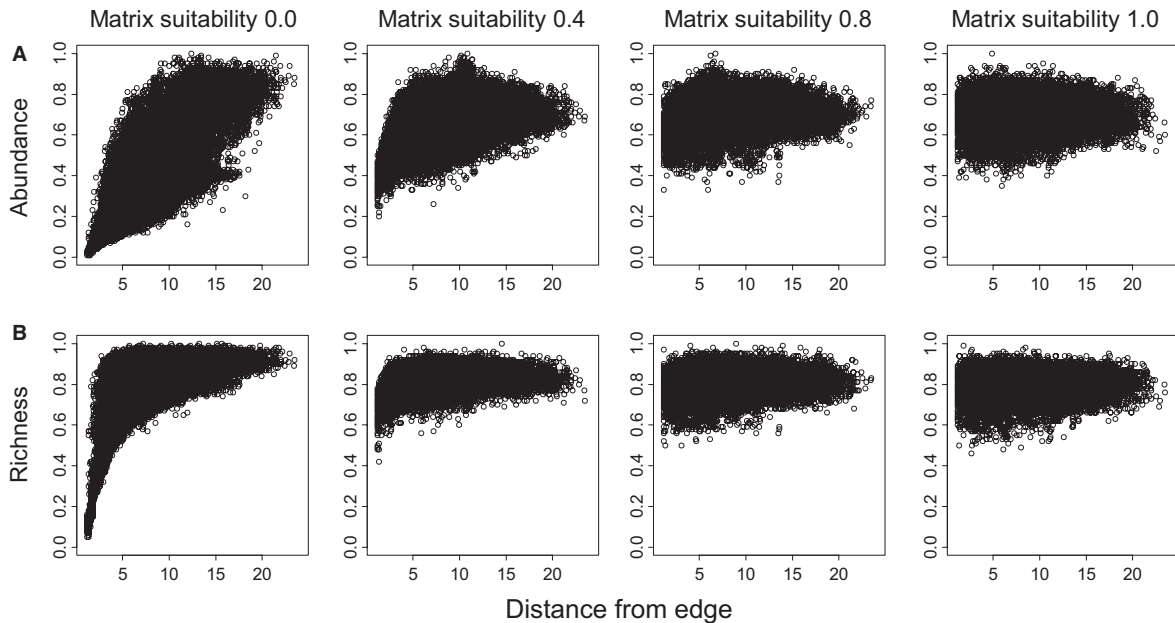


FIG. 5. Edge effects on (A) abundance and (B) species richness per habitat grid cell for different matrix suitability values, as predicted by the landscape model. Abundance and species richness are shown as proportional values, calculated separately for each matrix suitability value as (predicted value)/(maximum predicted value). The mean distance (in number of cells) of each cell from the border of the patch (or sample site) was quantified by considering the eight main directions surrounding each cell.

consistent increases in abundance and richness with patch size (abundance $r^2 = 0.69$, $P < 0.001$; richness $r^2 = 0.68$, $P < 0.001$; Fig. 9E, F). Observed and predicted abundance and richness values were significantly correlated (abundance $r^2 = 0.33$, $P = 0.008$; richness $r^2 = 0.34$, $P = 0.007$; Fig. 9I, J). The intercepts of the relationships between predicted and observed values differed significantly from 0, for both abundance (5.42 ± 1.91 [mean \pm SE], $t = 2.80$, $P = 0.01$) and richness (2.29 ± 0.82 , $t = 2.80$, $P = 0.01$). The slopes of these relationships differed significantly from 1 (abundance 0.39 ± 0.13 , $t = -4.61$, $P < 0.001$; richness 0.50 ± 0.16 , $t = -3.02$, $P = 0.007$).

For specialist species, predictions of Coleman's model were significantly correlated with observed values, but the fit (as judged from r^2 values) was lower than the fit between our model and observed values, for both abundance ($r^2 = 0.24$, $P = 0.03$) and richness ($r^2 = 0.25$, $P = 0.02$). The intercepts of the relationships between predicted and observed values differed significantly from 0, for both abundance (8.31 ± 1.42 , $t = 5.85$, $P < 0.001$) and richness (3.53 ± 0.65 , $t = 5.45$, $P < 0.001$). The slopes of these relationships differed significantly from 1, for both abundance (0.24 ± 0.10 , $t = -7.90$, $P < 0.001$) and richness (0.33 ± 0.13 , $t = -5.11$, $P < 0.001$).

For generalist species, observed abundance and richness did not vary significantly with patch size (abundance $r^2 = 0.07$, $P = 0.27$; richness $r^2 = 0.004$, $P = 0.77$). In contrast, the model predicted a reduction in both abundance and richness with increasing patch size

(abundance $r^2 = 0.48$, $P < 0.001$; richness $r^2 = 0.58$, $P < 0.001$; Fig. 9G, H). Observed values and values predicted by the model were positively but nonsignificantly correlated for both abundance ($r^2 = 0.11$, $P = 0.15$; Fig. 9K) and richness ($r^2 = 0.02$, $P = 0.51$; Fig. 9L). The intercepts of the relationships between predicted and observed values differed significantly from 0 (abundance 7.35 ± 3.06 , $t = 2.40$, $P = 0.03$; richness 2.09 ± 0.15 , $t = 13.46$, $P < 0.001$), and the slopes differed significantly from 1 (abundance 0.39 ± 0.26 , $t = -2.30$, $P = 0.03$; richness 0.05 ± 0.07 , $t = -12.81$, $P < 0.001$).

For generalist species, predictions of Coleman's model were negatively but nonsignificantly related to observed values, for both abundance ($r^2 = 0.11$, $P = 0.15$) and richness ($r^2 = 0.02$, $P = 0.51$). The intercepts of the relationships between predicted and observed values differed significantly from 0 (abundance 10.25 ± 1.06 , $t = 9.69$, $P < 0.001$; richness 2.33 ± 0.18 , $t = 13.16$, $P < 0.001$). The slopes were negative and differed significantly from 1 (abundance -0.13 ± 0.09 , $t = -12.46$, $P < 0.001$; richness -0.06 ± 0.08 , $t = -12.44$, $P < 0.001$).

DISCUSSION

Despite its simplicity and minimal assumptions, the landscape model produced realistic gradients of species abundance and richness across both simulated and real landscapes. More specifically, the model was able to generate realistic area, isolation, edge, and matrix effects in communities. Such outcomes were robust to

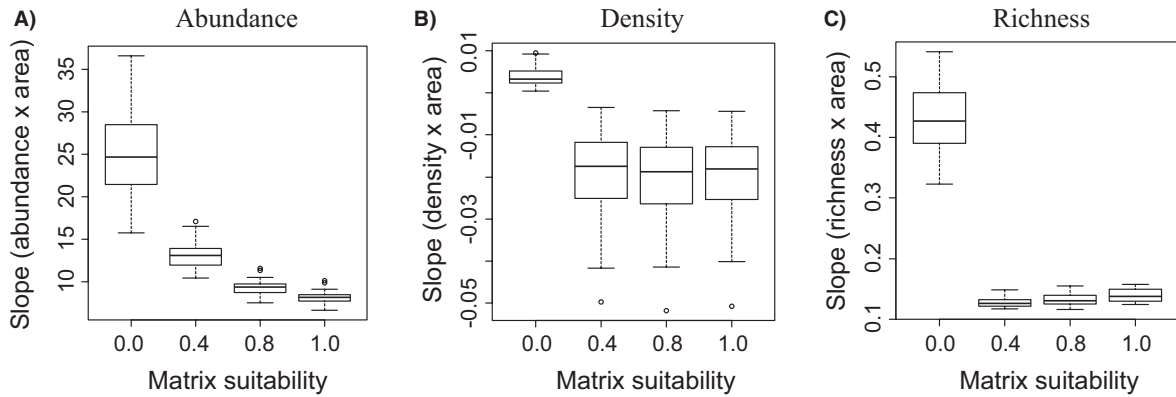


FIG. 6. Slopes of the relationship between patch area and (A) abundance, (B) density, and (C) species richness across 30 iterations of the landscape model for different matrix suitability values. Symbols are the median (horizontal line), ± 1 SE (box), 95% confidence intervals (vertical lines), and outliers (points) of the slopes across 30 iterations.

variations in habitat cover (10% and 30%), habitat configuration, home range size distribution, population sizes, and in the degree of intraspecific territorialism (see Appendices S1–S6). Variation in home range sizes incorporated the assumption that an individual's occupation of the landscape is subject to geometric constraints, with consequences for community abundance and richness, which have been so far largely neglected in the literature. Variation in matrix suitability confirmed that the matrix mediates area, isolation, and edge effects, and provided a common framework to study landscapes with different structures, from patchy to more homogeneous. To date, patchy and homogeneous landscapes have usually been studied rather separately by landscape ecologists, biogeographers, and macroecologists. Because the landscape model explicitly excludes many ecological processes, such as extinction, interspecific interactions, and variation in habitat quality within habitat patches, its ability to produce realistic gradients of abundance and richness in landscapes raises the possibility that such gradients are driven, at least in part, by simple probabilistic forces,

more specifically geometric constraints acting on the placement of home ranges across the landscape.

Model outcomes vs. empirical patterns

Although the landscape model is static, it nevertheless produced realistic species–area curves (Fig. 3C). This result reinforces the premise of the random placement model, which is that the species–area relationship may result at least in part from probabilistic processes, emerging even when extinction processes are not explicitly considered (Connor and McCoy 1979, Coleman et al. 1982, Bidwell et al. 2014). However, the predictions of the landscape model differed from predictions of the traditional random placement model, especially for small habitat patches.

The random placement model assumes that the number of individuals is always directly proportional to patch size (Coleman 1981), regardless of species' home range sizes or matrix suitability. This model does not consider the potential influence of matrix suitability because it was originally conceived for application in strictly patchy

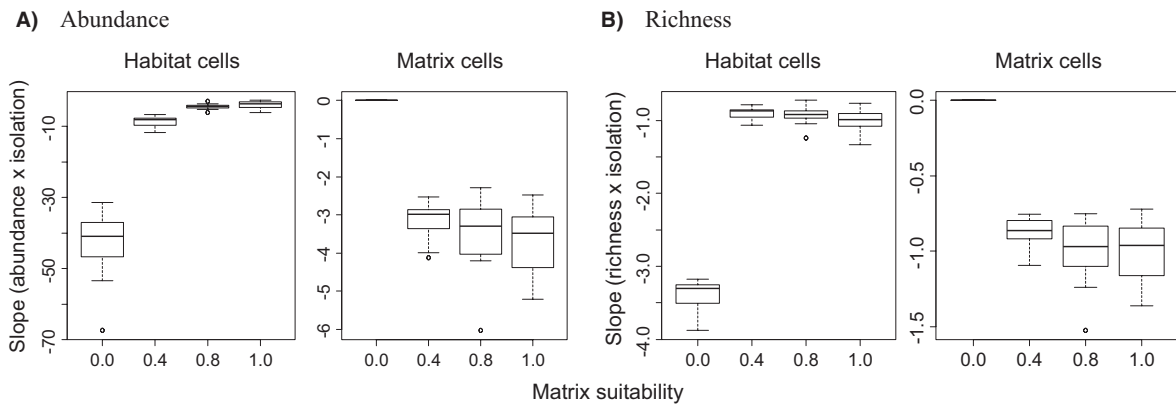


FIG. 7. Slopes of the relationships between cell isolation and (A) abundance or (B) species richness across 30 iterations of the landscape model. Values are shown separately for habitat and matrix cells and for different matrix suitability values. Symbols are the median (horizontal line), ± 1 SE (box), 95% confidence intervals (vertical lines), and outliers (points) of the slopes across 30 iterations.

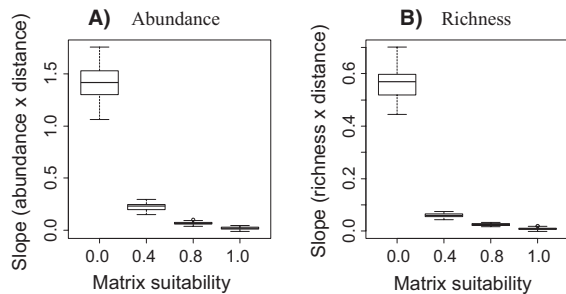


FIG. 8. Slopes of the relationships between the distance of each habitat cell from the borders of the patch and (A) abundance or (B) species richness, across 30 iterations of the landscape model. The mean distance from the borders was quantified by considering the eight main directions surrounding each cell. Symbols are the median (horizontal line), ± 1 SE (box), 95% confidence intervals (vertical lines), and outliers (points) of the slopes across 30 iterations of the model.

landscapes (island archipelagoes), where the matrix (water) is completely inhospitable for organisms. Because it ignores home range sizes, when compared to the landscape model, Coleman's (1981) model overestimates richness for patches that are too small to harbor the home ranges of some large-bodied species when the matrix is completely unsuitable to individuals. In contrast, when matrix suitability is relatively high (≥ 0.8), the random placement model underestimates richness for small patches, because it does not account for the presence of individuals whose home ranges are located in the matrix but also partially overlap with the habitat patch. Such individuals, which may use the matrix as a secondary habitat, increase population abundance within the patch (Bowers et al. 1996, Brotons et al. 2003), thereby increasing species richness.

For the same reasons, the landscape model and the random placement model differ in their predictions regarding density–area relationships. Whereas the random placement model predicts uniformity in population density across patches, the landscape model can generate negative or positive density–area relationships, depending on matrix suitability. Indeed, for mammals, both positive and negative density–area relationships have been documented in the literature (Bowers and Matter 1997, Connor et al. 2000, Brotons et al. 2003). Evidence compiled by Bowers and Matter (1997) and Brotons et al. (2003) suggest that these relationships tend to be positive for more isolated habitat patches, such as true islands, but negative or neutral for less isolated patches, in agreement with the landscape model.

The landscape model generated realistic species–area slopes (z values) that fell within the range observed in empirical studies. In a comprehensive review, Triantis et al. (2012) showed that z values known for islands range from 0.06 to 1.31, with a mean of $z = 0.32$, close to the values produced by the landscape model ($z = 0.40$) for landscapes with unsuitable matrix. For terrestrial patches, Watling and Donnelly (2006) documented mean

z values of 0.18, close to the values produced by the landscape model for landscapes with matrix suitability > 0 ($z = 0.14$).

Additionally, z values decreased as matrix suitability increased, in accordance with many empirical studies documenting higher z values for true islands compared to areas within terrestrial landscapes (MacArthur and Wilson 1967, Connor and McCoy 1979, Fahrig 2013). The higher z values for islands compared to habitat patches in terrestrial landscapes (the *island effect*; Fahrig 2013) have usually been attributed to a lower immigration rate on islands, due to their relative isolation (Connor and McCoy 1979, Watling and Donnelly 2006, Fahrig 2013). According to this hypothesis, in terrestrial landscapes, the more favorable matrix would allow higher immigration rates, increasing richness especially in small patches, both by increasing the number of transient species (MacArthur and Wilson 1967) and by decreasing extinction rates due to the rescue effect (Brown and Kodric-Brown 1977). In addition, a more favorable matrix is supposed to decrease species extinctions in small fragments by providing species with supplementary or complementary resources (Dunning et al. 1992, Gascon et al. 1999). In the landscape model, which is static, variation in z values was not caused by variation in extinction or immigration rates, but simply by variation in the probability of occupancy of the small habitat patches by individuals. The decrease in z values with the increase in matrix suitability is another realistic feature of the landscape model that is not predicted by the random placement model, which ignores variation in home range sizes and does not account for matrix suitability.

Effective isolation, as measured through the modified similarity index, had a negative effect on the abundance and richness of landscape cells, in accordance with an extensive empirical literature (see Fig. 1; Ewers and Didham 2006). When the matrix was at least partially suitable to individuals (suitability > 0), this effect occurred for both habitat and matrix cells. This result provides support for the “habitat amount hypothesis” (Fahrig 2013), which posits that species abundance and richness in a given point of the landscape should increase with the total amount of habitat in the local surroundings, even when this habitat is embedded in a low-quality matrix.

Isolation effects were stronger when matrix suitability was lower, and became progressively weaker as matrix suitability increased and landscape became more homogeneous, again in accordance with empirical studies (Bender and Fahrig 2005, Prevedello and Vieira 2010, Kennedy et al. 2011, Driscoll et al. 2013). The mediating role of the matrix on isolation effects is usually attributed to its effect on movement and dispersal of organisms, which are believed to affect immigration and extinction probabilities (Bender and Fahrig 2005, Kennedy et al. 2011, Driscoll et al. 2013). In the landscape model, isolation effects reflect simple probabilistic processes: the larger the number of cells of high suitability in the

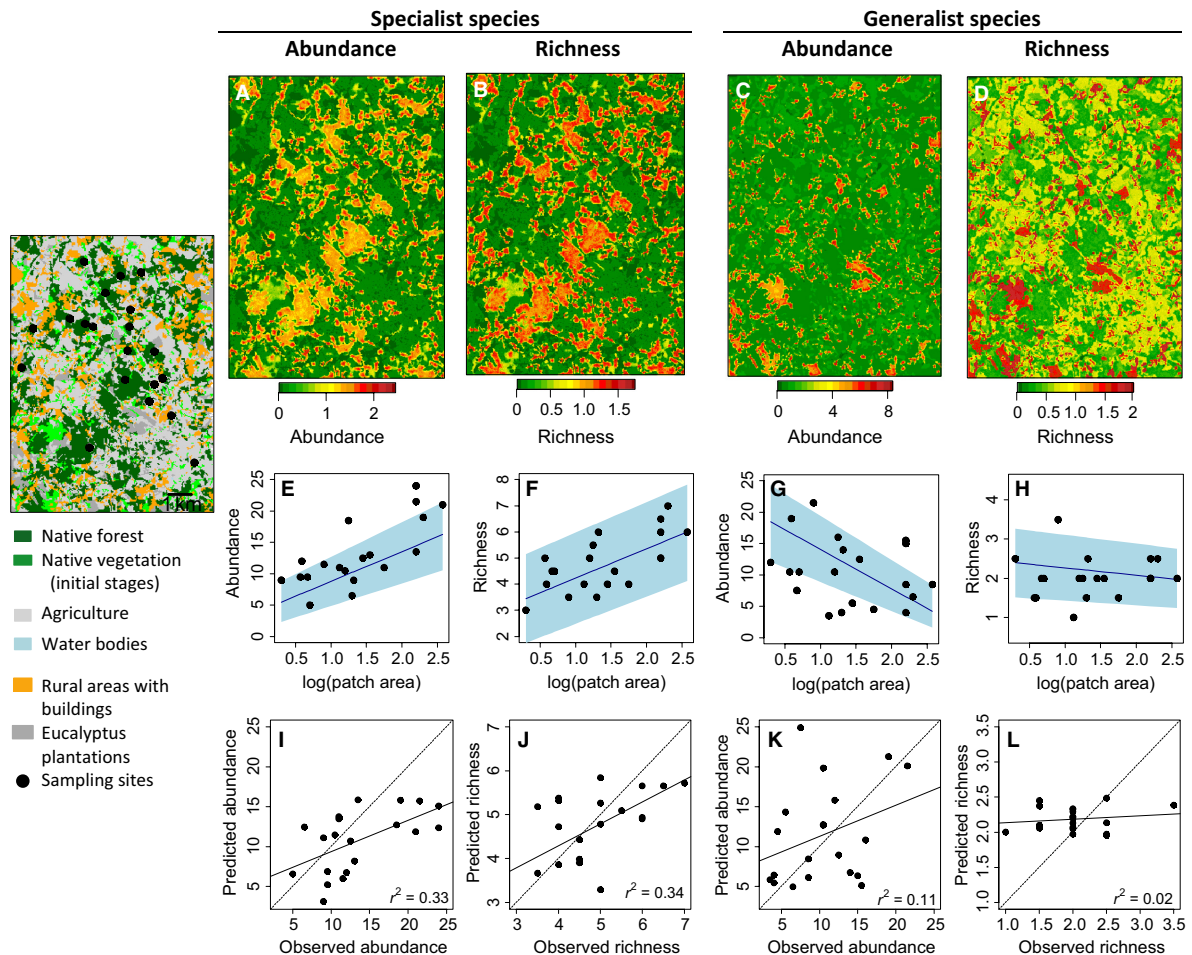


FIG. 9. Results of the application of the landscape model to small mammals of the Atlantic Forest, Brazil. The studied landscape is shown on the left. (A–D) Predicted abundance and species richness per grid cell for specialist and generalist species. (E–H) Variation of observed (points) and predicted (mean \pm 2 SD across 100 iterations, shaded area) abundance and species richness per sampling site with forest patch size. (I–L) Correlation between observed and predicted (mean across 100 iterations) abundance and richness per sampling site (r^2 = coefficient of determination). The dotted line depicts the 1:1 relationship.

neighborhood of a given focal cell, the higher is the probability of that focal cell being reached and occupied as a part of individuals' home ranges (see Fig. 4A). This explains why isolation effects emerged from the landscape model even when the landscape was homogeneous (see Fig. 4, column "matrix = 1.0"). In this case, cells located near the edges of the landscape had fewer neighbor cells than cells located at more central portions of the landscape and, as a consequence, had slightly lower abundance and richness. This is clearly another manifestation of the mid-domain effect (Colwell and Lees 2000), which therefore can have a role in mediating isolation effects if landscapes are surrounded by unsuitable areas (see, e.g., Tiwari et al. 2005). However, if this is not the case, researchers applying the model to real data should ensure that the landscape maps used in simulations are larger than the landscape area sampled, to avoid interference of this mid-domain effect on model predictions.

Although isolation had a clear effect on abundance and species richness at the scale of individual landscape cells, it had weaker effects at the scale of habitat patches (see Appendix S7). At this scale, isolation effects were obscured by variation in patch sizes, which were much more important determinants of abundance and species richness. When the analysis was restricted to equal-sized patches, isolation effects appeared, but were again relatively weak (see Appendix S7). The relative importance of patch isolation, especially as compared to patch size, has been the subject of debate in the literature (Beier et al. 2002, Fahrig 2003, 2013, Boscolo and Metzger 2011). In a comprehensive meta-analysis, Watling and Donnelly (2006) showed that patch size has consistent, positive effects on species richness, whereas isolation effects are much weaker. They suggested that this pattern could reflect the narrow range in patch isolation included in the original studies, and that isolation effects would be stronger if patch isolation was more variable. Accordingly, for real islands, isolation effects are

known to be stronger when different archipelagos located at different distances from mainland are compared, whereas isolation usually has little impacts on richness variation within a single archipelago (Connor and McCoy 1979, Triantis et al. 2012). It is possible that more consistent isolation effects would emerge from the landscape model if it were applied to very large landscapes encompassing a broader range of variation in patch isolation. On the other hand, it is also possible that isolation effects observed in real systems are in fact the result of a balance between immigration and extinction processes, as assumed by the equilibrium model and the neutral model, but ignored by the landscape model.

The landscape model produced clear gradients of abundance and richness from the edges to the interior of habitat patches, thus reproducing edge effects. Edge effects are usually attributed to variation in resources and conditions along the edge-to-interior gradient, such as food, vegetation structure, and density of predators (Lidicker 1999, Ries et al. 2004, Villaseñor et al. 2014). However, edge effects may also emerge from neutral community dynamics in bounded habitat patches (Rangel and Diniz-Filho 2005), or from simple geometric constraints acting on the placement of individual's home ranges (Prevedello et al. 2013). Prevedello et al. (2013) showed that geometric constraints tend to reduce abundance and richness near habitat boundaries even when habitat quality is homogeneous across habitat patches. This *geometric edge effect*, which is analogous to the classical mid-domain effect (Colwell and Lees 2000), occurs simply because habitat areas located near patch boundaries receive few (or any) individuals from the matrix. Prevedello et al. (2013) quantified the geometric edge effect only for habitat patches embedded in a completely unsuitable matrix, and suggested that this effect should become weaker as matrix suitability increased, a prediction supported by our simulations. The outcomes of the landscape model are also in accordance with many empirical studies, which have shown that matrix suitability regulates the intensity of edge effects (Perfecto and Vandermeer 2002; Ries et al. 2004, Villaseñor et al. 2014). This general agreement between model outcomes and expectations shows that the well-known influence of matrix suitability on edge effects is not necessarily mediated by changes in habitat quality near habitat edges, but potentially can result from simple geometric constraints.

Case study

Predictions of the landscape model were qualitatively in agreement with observed patterns in abundance and richness for specialist small mammal species. The model predicted consistent increases in abundance and richness of these species with increasing patch size, similarly to the general pattern observed with field data (Fig. 9E, F; see also Fig. 4 in Pardini et al. 2010), resulting in significant correlations between predicted and observed values, and slopes differing from 0. However, the model accounted

for only a limited fraction of the variability in observed values ($r^2 = 0.33$ for abundance and 0.34 for richness), and the intercept and slope differed significantly from 0 and 1, respectively.

In general, the model overestimated richness and abundance in smaller patches, and underestimated richness and abundance in larger patches (Fig. 9I–L). Such deviations between observed and predicted values can be attributed either to inaccuracies in model parameterization, i.e., inaccurate estimates of home range sizes, total abundance, and habitat suitability, or to the action of ecological processes unaccounted for by the model. Such processes might include ongoing extinction, which would reduce richness especially in smaller patches (Pardini et al. 2010) or a greater concentration of critical resources in larger patches, which would increase population densities as patch sizes increase (Root 1973, Connor et al. 2000). These processes could explain why the model overestimated richness and abundance in smaller patches, and underestimated richness and abundance in larger patches. Other ecological factors, including interspecific competition and conspecific attraction or aggregation (Püttker et al. 2015), could contribute to variability in observed data unexplained by the landscape model.

Although the fit of the landscape model to data was only partially satisfactory, it outperformed Coleman's (1981) model by generating predictions that matched more closely observed patterns. For specialist species, the model fitted the data better than Coleman's model, as judged from the higher r^2 values and slopes, and lower intercepts. For generalist species, both models performed poorly on a quantitative basis, but predictions of the landscape model were qualitatively more realistic, at least for abundance. The landscape model predicted a decrease in abundance with increasing patch size, reproducing the tendency observed with field data (Fig. 6G), whereas Coleman's model predicted an increase with patch size, resulting in negative correlations between observed and predicted values.

Implications and potential applications of the landscape model

The main contribution of the landscape model is to show that the most common landscape patterns of biodiversity may result, at least in part, from simple probabilistic processes, more specifically geometric constraints acting on home range placement. Such geometric constraints affect the likelihood that different portions of the landscape are occupied by individual home ranges, generating predictable gradients in species abundance and richness. The potential importance of individual-level geometric constraints as a causal mechanism of landscape patterns of biodiversity has been largely ignored so far, with the exception of recent studies on edge effects (Prevedello et al. 2013, Ribeiro et al. 2016). By showing the potentially large influence of such geometric constraints,

our simulations suggest that area, isolation, edge, and matrix effects are to be expected even in the absence of strong influences of many ecological factors frequently implicated as their causal mechanisms, such as extinction, interspecific interactions, and variation in habitat quality within habitat patches (Ries et al. 2004, Ewers and Didham 2006, Triantis et al. 2012, Driscoll et al. 2013).

Geometric constraints have received much attention in macroecology and biogeography, in studies investigating large-scale patterns in species richness, such as latitudinal and altitudinal gradients (Colwell and Lees 2000, Colwell et al. 2004, Gotelli et al. 2009). The suggestion that geometric constraints, acting on the placement of species' geographical ranges, could produce predictable gradients in species richness fueled substantial debate among researchers, leading to important theoretical and methodological advances in macroecology and biogeography (Colwell et al. 2004).

Analogously, we believe the recognition that individual-level geometric constraints can produce realistic gradients at smaller (landscape) scales has important implications that may advance substantially knowledge on landscape patterns of biodiversity. First, it suggests that individual-level geometric constraints per se should be acknowledged as a potential causal mechanism of area, isolation, edge, and matrix effects. Incorporation of geometric constraints into explanatory models, in combination with other likely causal mechanisms, may assist identifying the true probabilistic and ecological drivers of such effects, helping to resolve ongoing debates on the causal mechanisms of landscape patterns of biodiversity.

Second, the recognition that individual-level geometric constraints may generate predictable gradients contradicts an assumption implicit in many tests of area, isolation, edge, and matrix effects, namely that species abundance and richness should be homogeneously distributed within and among habitat patches, in the absence of strong influences of extinction processes, interspecific interactions, and variation in habitat quality within patches (e.g., Ries et al. 2004, Pardini et al. 2010). Geometric constraints are likely to produce gradients in species abundance and richness in landscapes, which should be taken into account when designing and interpreting statistical tests of area, isolation, edge, and matrix effects.

Finally, the recognition that individual-level geometric constraints may affect abundance and richness may assist predicting the likely impacts of future landscape changes on biodiversity. For example, creation of roads, removal of particular habitat patches, or changes in the management of the matrix are all likely to influence the occurrence and intensity of geometric constraints, which in turn may affect biological communities in somewhat predictable ways.

Although the qualitative fit of the landscape model to general biodiversity patterns observed in the literature (Fig. 1A; Ewers and Didham 2006) is good, it remains to be seen how well it will function when it is fine-tuned to test area, isolation, edge, and matrix effects in different assemblages

and landscapes. As our case study illustrates, the model can be parameterized with information on home range, abundance and matrix use from empirical studies, generating predictions on a broad range of patterns that can be directly compared to real data. For cases in which the landscape model fails to predict observed patterns, consistent deviations from the model may provide clues to the mechanisms that are in operation, as exemplified by the consistent over- and underestimation of richness in small and large patches, respectively, in the real landscape we analyzed. Such achievements are an important contribution of simple (null) models (Gotelli and Graves 1996, Gotelli et al. 2009), including the random placement model and the mid-domain effect model (Coleman et al. 1982, Colwell and Lees 2000, Bidwell et al. 2014). By encompassing the central assumptions of these two models, but still retaining their simplicity, the landscape model is likely to provide a more general and proper baseline model for the study of landscapes. It may also serve to strengthen the conceptual links between landscape ecology, macroecology, community ecology, and biogeography, which is certainly desirable to achieve a more thorough understanding of the variation in biodiversity at different spatial scales.

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