



Importance of estimating matrix quality for modeling species distribution in complex tropical landscapes: a test with Atlantic forest small mammals

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Information to guide decision making is especially urgent in human dominated landscapes in the tropics, where urban and agricultural frontiers are still expanding in an unplanned manner. Nevertheless, most studies that have investigated the influence of landscape structure on species distribution have not considered the heterogeneity of altered habitats of the matrix, which is usually high in human dominated landscapes. Using the distribution of small mammals in forest remnants and in the four main altered habitats in an Atlantic forest landscape, we investigated 1) how explanatory power of models describing species distribution in forest remnants varies between landscape structure variables that do or do not incorporate matrix quality and 2) the importance of spatial scale for analyzing the influence of landscape structure. We used standardized sampling in remnants and altered habitats to generate two indices of habitat quality, corresponding to the abundance and to the occurrence of small mammals. For each remnant, we calculated habitat quantity and connectivity in different spatial scales, considering or not the quality of surrounding habitats. The incorporation of matrix quality increased model explanatory power across all spatial scales for half the species that occurred in the matrix, but only when taking into account the distance between habitat patches (connectivity). These connectivity models were also less affected by spatial scale than habitat quantity models. The few consistent responses to the variation in spatial scales indicate that despite their small size, small mammals perceive landscape features at large spatial scales. Matrix quality index corresponding to species occurrence presented a better or similar performance compared to that of species abundance. Results indicate the importance of the matrix for the dynamics of fragmented landscapes and suggest that relatively simple indices can improve our understanding of species distribution, and could be applied in modeling, monitoring and managing complex tropical landscapes.

Modeling, monitoring and managing complex human dominated landscapes is a major concern, though a difficult goal in applied conservation sciences. This is especially the case in the tropics, since biodiversity or ecosystem services cannot be conserved in the long run only by protecting isolated and sparse reserves (DeFries et al. 2005, Soares-Filho et al. 2006). The understanding of processes and patterns in fragmented landscapes requires taking into account the suitability of altered habitats around remnants (i.e. the matrix habitats) for the occurrence or dispersal of organisms. This often involves, however, detailed and long term data on the biology of species, which, particularly in the tropics, are not available and are time-consuming to gather. Moreover, few empirical studies have investigated if simple indices of matrix quality can improve the explanatory power of landscape structure variables in relation to the distribution of species in fragmented tropical forest landscapes.

Habitat loss and habitat subdivision or fragmentation (Fahrig 2003) occur simultaneously in real landscapes and lead to changes in landscape connectivity, defined as the capacity of the landscape to facilitate biological fluxes (Tischendorf and Fahrig 2000). Although landscape connectivity depends on several factors, the suitability of matrix habitats surrounding remnants for the occurrence or dispersal of organisms has been comparatively less studied than the role of corridors. This is, in part, because the matrix of altered habitats has been considered initially as homogeneous and inhospitable by island biogeography and metapopulation theories (Vandermeer and Carvajal 2001, Haila 2002, Jules and Shahani 2003, Kupfer et al. 2006).

Recent simulation studies, however, have shown that in more heterogeneous landscapes, patch size and isolation are poor predictors of patch immigration rate (Bender and Fahrig 2005), that spatial arrangements of habitat patches of varying quality influence the probability of species

survival and dispersal, and that frequently used models of dispersal may have a poor performance in highly fragmented landscapes (Gardner and Gustafson 2004). Simple metrics of area and, most commonly, of isolation, such as the often used patch size and the euclidean distance among habitats, may present low explanatory power for species richness or abundance (Debinski and Holt 2000, Winfree et al. 2005) and colonization or dispersal (Moilanen and Nieminen 2002, Bender et al. 2003, Tischendorf et al. 2003, Winfree et al. 2005).

Empirical studies have clearly demonstrated that the matrix works as a mosaic of units with different degrees of suitability for the occurrence of different species (Perfecto and Vandermeer 2002, Daily et al. 2003, Pardini 2004, Antongiovanni and Metzger 2005, Wijesinghe and Brooke 2005, Umetsu and Pardini 2007) or for the dispersal of individuals (Ricketts 2001, Gobeil and Villard 2002, Schooley and Wiens 2004, Revilla et al. 2004, Stevens et al. 2004). In fact, the variability of responses to altered habitats is broad not only among distinct taxonomic groups (Gascon et al. 1999), but also within one guild (Antongiovanni and Metzger 2005) or even among closely-related species (Ricketts 2001). Nevertheless, most empirical studies on the influence of landscape structure on populations or communities did not consider the quality of matrix habitats (Jules and Shahani 2003, Bender and Fahrig 2005).

Another fundamental aspect for understanding the influence of landscape structure on ecological patterns and processes is the spatial scale considered (Vos et al. 2001). Differences in the capacity of dispersal (Bowman et al. 2001, 2002, Bender et al. 2003), foraging patterns (Steffan-Dewenter et al. 2002), seed dispersal syndromes (Metzger 2000), among others, determine the scale at which species respond to landscape structure. Metrics that account for adequate scales have a better explanatory capacity in comparison to those that use inappropriate spatial scales or that disregard them (Moilanen and Nieminen 2002, Bender et al. 2003).

Incorporating matrix quality and considering the importance of spatial scale in modeling is particularly urgent in tropical landscapes, where urban and agricultural frontiers are still expanding in a largely unplanned manner, with potential negative and irreversible effects on biodiversity and ecosystem processes (Soares-Filho et al. 2006, Oliveira Filho and Metzger 2006). Non-flying small mammals (small-bodied rodents and marsupials with <1 kg) comprise the most diversified ecological group of neotropical mammals (Fonseca et al. 1996, Costa et al. 2005). They are good indicators both of habitat disturbance (Pardini 2004, Wijesinghe and Brooke 2005, Lambert et al. 2006, Umetsu and Pardini 2007) and fragmentation (Castro and Fernandez 2004, Pardini et al. 2005) and play an important role in forest regeneration (Brewer and Rejmanek 1999). On the other hand, some generalist species which benefit from deforestation (Umetsu and Pardini 2007) are important vectors of human diseases (Katz et al. 2001). Their short life cycles, easy capture and relatively well-known taxonomy make small mammals a potential group for studying and modeling the effects of human activities on biodiversity in tropical forest landscapes.

There is no available information on the scale tropical small mammal species respond to landscape structure. Daily movements vary among species, but for most of them distances around 50 m are frequent, while long-distance movements (longer than 100 m) are rare (Gentile and Cerqueira 1995, Pires et al. 2002). The average long-distance movements for small mammal species in a temperate region varied from 224 to 370 m, values which are close to the scale of species response to landscape structure (133 and 533 m; Bowman et al. 2001) or the scale of variation (between 250 and 1000 m) in population density of these species (Bowman et al. 2001).

Home ranges of tropical small mammals are small, varying from 1 ha for the largest-bodied marsupials to <0.5 ha for most rodents in the Atlantic forest (Bergallo 1994, 1995, Bergallo and Magnusson 2004), indicating, based on the relationship of distance of dispersal to the squared root of home range size in mammals (Bowman et al. 2002), that the dispersal ability of these animals is low. Moreover, the majority of these species are able to occupy forests under some degree of disturbances (Pardini 2004, Pardini et al. 2005). Thus, it is reasonable to assume that the occurrence of populations in altered habitats of the matrix would have a more important role for the connectivity of small mammal populations than the periodic dispersal of individuals among remnants through the matrix.

In this study, using the distribution and abundance of small mammals in 20 forest remnants and 16 sites in the four main altered habitats of the matrix in a fragmented Atlantic forest landscape, we investigated how the explanatory power of models describing species distribution in forest remnants varies between landscape structure variables that do or do not incorporate matrix quality. We assumed that information on the relative abundance of species, gathered through standardized sampling in different habitat types of a heterogeneous landscape, is useful as an index of matrix quality. Additionally, we investigated the importance of spatial scale for analyzing the influence of landscape structure. We hypothesized that the inclusion of matrix quality will increase the explanatory power of the models of landscape structure on small mammal distribution and that the scale to which species respond to landscape structure will vary among small mammal species.

Material and methods

Study area and sites

The Atlantic forest, the second largest tropical rainforest in the American continent, covered an area of >1.5 million km² distributed mainly along the Brazilian coast and has been reduced to <7% of its original area (Tabarelli et al. 2005).

The study area is located in the Ibiúna Plateau, municipality of Ibiúna, State of São Paulo, Brazil (Fig. 1). The altitude in the region ranges from 850 to 1100 m (Ross and Moroz 1997). The mean maximum temperature is 27°C and the mean minimum temperature is 11°C. Rainfall is ca 1300–1400 mm yr⁻¹ and is seasonally variable, with the driest and coldest months between April

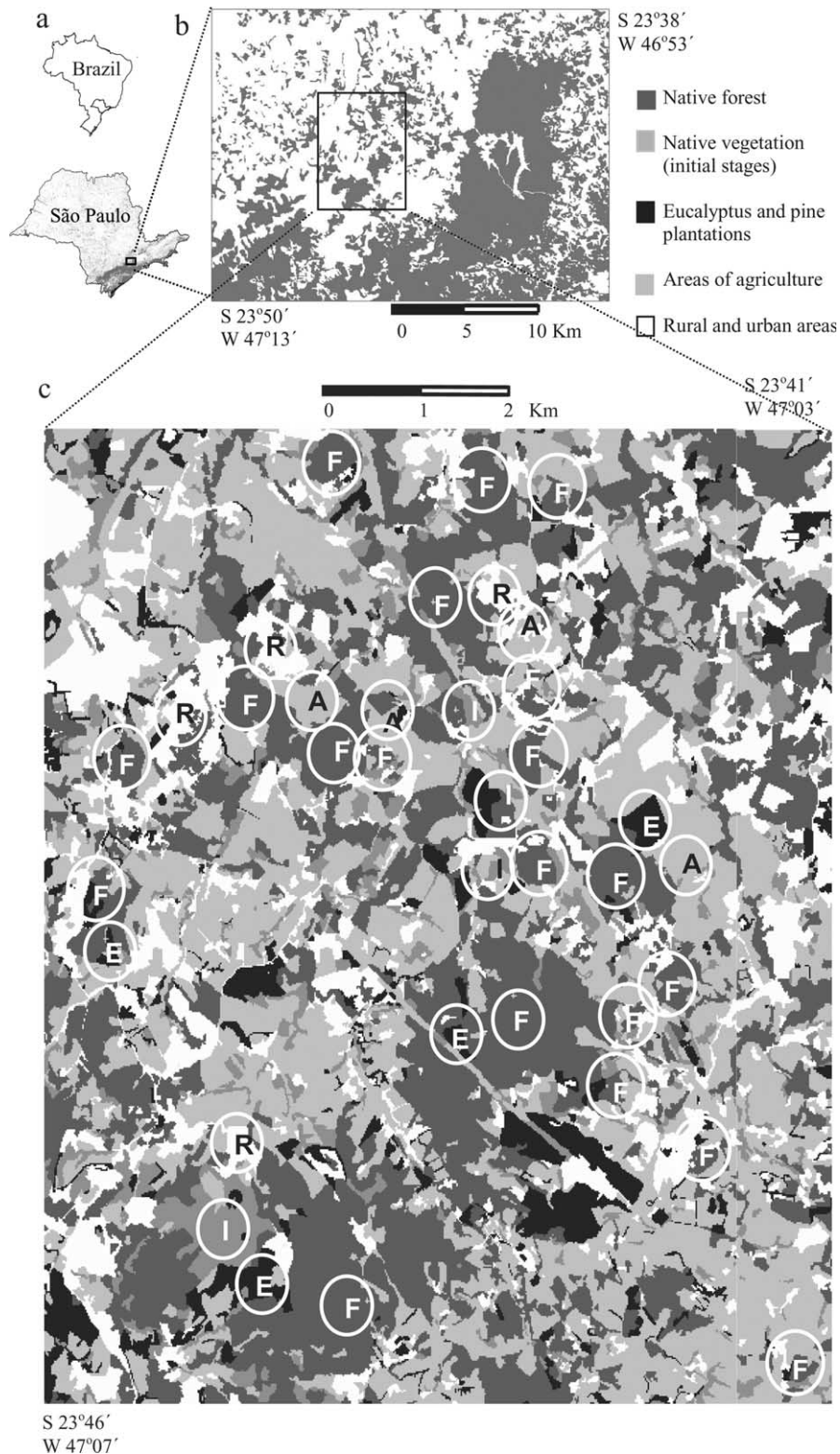


Figure 1. (a) Map of the state of São Paulo, Brazil, showing the distribution of current remnants of Atlantic forest and the location of the Ibiúna Plateau. (b) Distribution of forest remnants in the region and location of the studied fragmented landscape. (c) Distribution of the main habitats types in the fragmented landscape and position of the habitat patches where the 36 study sites were located, F – forest remnants, I – native vegetation in initial stages of regeneration, E – eucalyptus plantations, A – areas of agriculture, R – rural areas with buildings.

and September. Vegetation in the region is a transition between the coastal Atlantic rain forest and the Atlantic semi-deciduous forest, classified as “Lower Montane Atlantic Rain Forest” by Oliveira-Filho and Fontes (2000).

The fragmented landscape under study comprises 10 000 ha and harbors 31% of native forest (native secondary vegetation in intermediate stages of regeneration). Surrounding forest remnants, areas of agriculture (38% of the landscape), rural and urban areas with buildings (14.5%), native vegetation in initial stages of regeneration (7.5%), and homogeneous pine and eucalyptus plantations (7%) are the predominant habitat types (Fig. 1). Mining areas and water bodies cover a small area of the studied landscape.

The small mammal community was sampled at 36 sites, 20 of which were located in forest remnants and 16 in the altered habitats of the matrix (Fig. 1). To assure a large range of forest remnant size, we first selected the five largest forest remnants of the landscape (> 50 ha, $X = 150.48$ ha; $SD = 83.73$). Among smaller remnants, we selected sites based on presence/absence of forest corridors to large remnants, remnant size (small – < 5 ha, and medium-sized – 10 – 50 ha), and distance to large remnants (Pardini et al. 2005). The 20 forest remnants included a wide variation in size (2 – 275 ha) and in the four predominant types of surrounding matrix habitats. Considering an 800-m radius circumference around sampling sites in remnants, proportion of native forest varied from 11.0 to 77.6% ($X = 37.5$; $SD = 16.9$), areas of agriculture from 14.5 to 72.3% ($X = 38.0$; $SD = 12.7$), rural and urban areas with buildings from 2.4 to 29.9% ($X = 13.5$; $SD = 7.1$), native vegetation in initial stages of regeneration from 0.5 to 11.8% ($X = 6.6$; $SD = 2.8$), and homogeneous pine and eucalyptus plantations from 0.8 to 12.3% ($X = 4.4$; $SD = 3.5$).

Among the sites in the matrix, we selected four in each of the four predominant types of matrix habitats surrounding forest remnants: areas used for agriculture that at the time of sampling were cultivated (plantations of vegetables or corn) or fallow for less than a year; rural areas where buildings, such as houses, greenhouses and storages are located; native vegetation in initial stages of regeneration, represented by shrubby vegetation; and homogeneous eucalyptus plantations with no or sparse native understory (Umetsu and Pardini 2007). Considering the small size and the irregular shape of most patches in the matrix, the influence from surrounding habitat types was reduced by locating sites in the largest patches adjacent to forest remnants: areas of agriculture ($X = 111.70$ ha; $SD = 92.48$), native vegetation in initial stages of regeneration ($X = 20.52$ ha; $SD = 24.89$), rural areas with buildings ($X = 9.37$ ha; $SD = 10.10$), and eucalyptus plantations ($X = 11.59$ ha; $SD = 11.71$). Within those patches, the two parallel trap lines were positioned 20 and 40 m from the nearest forest edge, except sites in rural areas with buildings where trap location was constrained by human usage, passage and activities (Umetsu and Pardini 2007).

Data collection of small mammals

At each site, we set two parallel lines of Sherman traps of two different sizes ($37.5 \times 10 \times 12$ cm; $23 \times 7.5 \times 8.5$ cm). Trap lines were 165-m long, and 20 m apart. On each line,

we established 12 trap stations at 15-m intervals, totaling 24 stations at each site. One small and one large trap were set in each station, totaling 48 traps at each study site. At sites with shrubby or tree vegetation (forest remnants, areas in initial stages of regeneration, and eucalyptus plantations), we set one trap on the ground and one 1.0-m high on the vegetation and the height of small and large traps was alternated in adjacent stations. In areas of agriculture, both traps in each station were set on the ground and in rural areas with buildings, the 48 traps were distributed in relatively protected places, because a systematic distribution was not feasible due to the presence of people, domesticated animals and cars. Traps were baited with banana and a mixture of peanut butter, cornmeal and sardines. We used different sizes and heights of location of traps in order to include, respectively, large and arboreal species. This capture protocol proved to be efficient in capturing neotropical small mammals (Pardini 2004, Pardini and Umetsu 2006, Umetsu et al. 2006).

Sites in forest remnants were sampled between July 2003 and April 2004 for 21 d divided in three capture sessions of seven days each, totaling an effort of 1008 trap-nights at each site, and 20 160 trap-nights in forest remnants. Sites in the matrix were sampled in August 2004 for seven consecutive days, totaling an effort of 336 trap-nights at each site and 5376 trap-nights in the matrix. The specimens captured were marked with numbered metallic ear-tags (National Band and Tag, Newport, KY) and were then released.

Indices of habitat quality

In order to calculate the indices of quality for the different habitats of the landscape, we considered that the quality of a habitat is directly related to the abundance or occurrence of small mammal species and used the capture results of standardized 7-d samplings carried out in 2004 in the four largest forest remnants and four largest patches of each of the four predominant types of matrix habitats. We calculated two indices of quality, one corresponding to the abundance (mean number of captured individuals among the four replicates) and the other corresponding to the occurrence (presence of at least one individual) for each small mammal species in each habitat type. Mining areas and water bodies, which comprise a small area in the landscape, were considered as unsuitable for the occurrence of small mammals.

Landscape structure surrounding forest remnants

We quantified two types of variables for each of the 20 forest remnants in different spatial scales: habitat quantity and habitat connectivity based on the distance and size of surrounding habitat patches. For each type, we calculated one metric that considers forest remnants as equally suitable and all matrix habitats as unsuitable for all small mammal species, and another that takes into account the variation in quality among habitats for each small mammal species.

Habitat quantity was calculated as the area of habitat within a circumference of defined radius (200, 400 or

800 m) around the center of sampling sites in forest remnants, using the formulae:

Habitat quantity (not considering matrix quality) = a

where a = total area of native forest within the circumference around the center of sampling sites;

$$\text{Habitat quantity (considering matrix quality)} = \sum_{i=1}^5 a_i \cdot Q_i$$

where a_i = total area of habitat i within the circumference around the center of sampling sites, and Q_i = index of quality for habitat i for each small mammal species.

Habitat connectivity was calculated considering the size and the distance of habitat patches within a defined search radius (50, 100, 200 or 400 m) from the edge of sampled forest remnants, using the formulae:

Habitat connectivity (not considering matrix quality)

$$= \sum_{j=1}^n \frac{a_j}{h_{fj}^2}$$

where a_j = area of forest patch j within the search radius from the edge of the sampled forest remnant, and h_{fj} = edge-to-edge distance between the sampled forest remnant and forest patch j (computed from cell centers). This metric corresponds to the Proximity index (PROX) applied to forest class presented in McGarigal and Marks (1995).

Habitat connectivity (considering matrix quality)

$$= \sum_{i=1}^5 \sum_{j=1}^n \frac{a_{ij} \cdot Q_i}{h_{ij}^2}$$

where a_{ij} = area of patch j of habitat type i within the search radius from the edge of the sampled forest remnant, h_{ij} = edge-to-edge distance between the sampled forest remnant and patch j of habitat type i (computed from cell centers), and Q_i = index of habitat quality for habitat i for each small mammal species.

We did not consider larger spatial scales to avoid too great a superposition between the areas surrounding the distinct study sites. Scales for connectivity are smaller than for habitat quantity, because the former considered the inter-patch distances from the edges of a focal forest remnant while the latter is calculated in circumferences of

different radii around the center of sampling sites in remnants.

All metrics were calculated using the program FRAG-STATS ver. 3.3 based on a land cover map drawn from the interpretation of aerial photographs dated from 2000, in a 1:10 000 scale, and with an accuracy of >88% (Silva et al. 2007).

Statistical analyses

The influence of different landscape structure variables calculated at varying spatial scales on the abundance of small mammal species in the 20 forest remnants was investigated using simple linear regressions with Poisson error and log link, using R 2.3.0 (R Development Core Team 2006). The likelihood quantifies how consistent a particular regression model (estimated slope and intercept) is with the observations and the likelihood ratio provides a direct measure of the strength of evidence in support of the best model (Royall 2004) and is more conveniently expressed as the difference between the logarithms of the likelihoods (Hilborn and Mangel 1997). We subtracted the log-likelihood of the intercept model (null model) from the log-likelihood of each Poisson regression model to obtain a corrected log-likelihood which corresponds solely to the addition of an independent variable in the regression model. Differences between log-likelihoods of models ≥ 2 were considered to indicate that the best model was strongly supported by the data (Burnham and Anderson 2002).

Results

Distribution of small mammals in the landscape and habitat quality

The sampling effort of 20 160 trap-nights yielded 10 species of small mammals in the 20 forest remnants in Ibiúna. Both *Monodelphis americana*, a rare species, and *Gracilinanus microtarsus* were not captured in the 7-d sampling carried out in 2004 in the four largest remnants and were thus not analyzed here. *Akodon montensis* and *Marmosops incanus* were the species with the widest distributions in the region, present in 18 out of 20 forest remnants and represented by 164 and 88 captured individuals in remnants (Table 1). *Euryoryzomys russatus* and *Micoureus paraguayanus* showed

Table 1. Number of remnants where small mammal species were found, number of captured individuals in remnants (in parentheses) and indices of habitat quality (Q_i) corresponding to the occurrence or abundance (in parentheses) of species in each habitat type in the Ibiúna Plateau, Brazil.

Species	Number of forest remnants where the species occurs and number of individuals	Indices of habitat quality (Q_i)				
		Forest remnants	Vegetation in initial stages	Eucalyptus plantations	Rural areas with buildings	Areas of agriculture
<i>Euryoryzomys russatus</i>	4 (13)	1 (0.25)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
<i>Didelphis aurita</i>	16 (54)	1 (0.50)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
<i>Delomys sublineatus</i>	12 (35)	1 (1.00)	1 (0.50)	0 (0.00)	0 (0.00)	0 (0.00)
<i>Marmosops incanus</i>	18 (88)	1 (2.00)	1 (0.25)	0 (0.00)	0 (0.00)	0 (0.00)
<i>Sooretamys angouya</i>	12 (18)	1 (0.75)	1 (1.00)	0 (0.00)	0 (0.00)	0 (0.00)
<i>Oligoryzomys nigripes</i>	14 (40)	1 (0.25)	1 (3.75)	1 (6.25)	1 (0.50)	1 (1.25)
<i>Akodon montensis</i>	18 (164)	1 (1.25)	1 (14.75)	1 (5.75)	1 (1.50)	1 (0.75)
<i>Micoureus paraguayanus</i>	2 (5)	1 (0.50)	0 (0.00)	1 (0.25)	0 (0.00)	0 (0.00)

the narrowest distributions, occurring in four or fewer remnants and represented by 13 and 5 captured individuals in remnants (Table 1).

Among the eight species that occurred in the largest forest remnants, only *Didelphis aurita* and *E. russatus* did not occur in any of the four habitats of the matrix (Table 1). Thus, for these species, the landscape structure variables did not vary among metrics considering or not the quality of matrix habitat. Six species were present in at least one type of matrix habitat and only *A. montensis* and *Oligoryzomys nigripes* were present in all habitats types (Table 1). Among matrix habitats, open anthropogenic habitats (rural areas with buildings and areas of agriculture) harbored the smallest (2) number of small mammal species, and native vegetation in initial stages of regeneration harbored the highest (5) number of small mammal species (Table 1). Matrix habitats also harbored five species from open

Brazilian biomes, such as *Calomys tener* and *Necomys lasiurus*, and three introduced species, *Rattus rattus*, *Rattus norvegicus* and *Mus musculus* (Umetsu and Pardini 2007), which were not recorded in forest remnants and are not analyzed here.

Landscape structure variables and the distribution of small mammals in forest remnants

For *E. russatus* and *D. aurita*, the two species that did not occur in the matrix, the models of forest quantity presented higher explanatory power across most spatial scales (with the exception of *E. russatus* at 200 m) than the models of forest connectivity (differences in log-likelihood > 2, Fig. 2). The Poisson regression models for *D. aurita* were significant only for forest quantity, while the models for

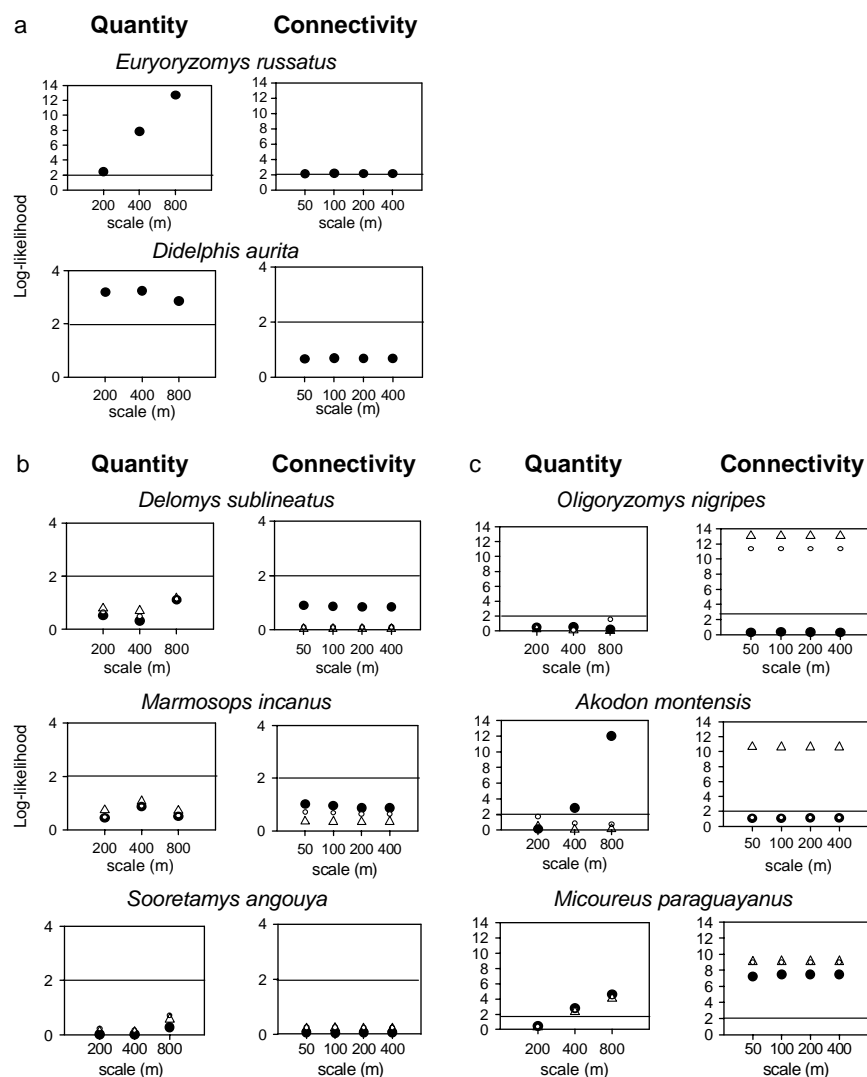


Figure 2. Log-likelihood values for Poisson regressions of the abundance of small mammal species in 20 forest remnants against forest quantity or connectivity (full circles) and habitat quantity or connectivity (using as indices of matrix quality both species occurrence – triangles, or abundance – empty circles) measured at varying spatial scales in the Ibiúna Plateau, Brazil. Log-likelihood of the intercept model (null model) was subtracted from the log-likelihood of each regression model, so that the log-likelihood of the null models was set to zero and the line indicates a difference of 2 from the null model in all graphics. (a) Species that did not occur in the matrix. (b) Species that occurred just in native vegetation in initial stages of regeneration. (c) Species that occurred in matrix habitats other than native vegetation in initial stages of regeneration.

E. russatus were significant for both forest quantity and forest connectivity (Table 2 and 3). The abundance of *D. aurita* decreased significantly with the increase in forest quantity across all spatial scales (Table 2, Fig. 2). Conversely, the abundance of *E. russatus* increased significantly with the increase in forest quantity and connectivity across all spatial scales (Table 2 and 3, Fig. 2).

For three of the six species that occurred in at least one type of matrix habitat (*D. sublineatus*, *M. incanus* and *Sooretamys angouya*), landscape variables (both of habitat quantity or connectivity) including or not matrix quality and measured at different spatial scales did not result in strong improvement of the explanatory power of the Poisson regression models in relation to the null model (differences in log-likelihood <2, Fig. 2). None of these models were significant (Table 2–4).

For the three other species that occurred in at least one type of matrix habitat (*A. montensis*, *O. nigripes* and *M. paraguayanus*) the explanatory power varied strongly among models (differences in log-likelihood >2, Fig. 2). Across most of the spatial scales considered (with one exception for one species), models of connectivity considering matrix quality were better than both models of connectivity that did not consider matrix quality and models of habitat quantity considering or not matrix quality (differences in log-likelihood >2, Fig. 2). Among the models of habitat connectivity, the use of the metric of habitat quality considering species occurrence resulted in better (for *O. nigripes* and *A. montensis*) or similar (for *M. paraguayanus*) models compared to the use of the metric considering species abundance (Fig. 2). For *O. nigripes* and *A. montensis*, models of connectivity were only significant when considering the quality of the matrix, while for *M. paraguayanus*, the models of connectivity considering only forest as habitat were already significant, but the explanatory power improved when considering matrix quality (Table 3 and 4). In all these significant models (all three species in all spatial scales), abundance was positively influenced by connectivity (Table 3 and 4).

On the contrary, for none of these three species, considering the quality of matrix habitats increased the explanatory power of the models of habitat quantity (differences in log-likelihood <2, Fig. 2). Moreover, while for *O. nigripes* none of the habitat quantity models were consistently better than the null model nor were significant, only few habitat quantity models were stronger than the null models or were significant for *A. montensis* (considering the matrix as unsuitable at 400 and 800 m) and for *M. paraguayanus* (all models at 400 and 800 m) (Fig. 2, Table 2). It is noteworthy that the significant relationship of *A. montensis* with habitat quantity was negative, contrary to the observed for the habitat connectivity models described above (Table 2 and 4).

Among habitat quantity models, the explanatory power of the models of three species (*A. montensis*, *M. paraguayanus* and *E. russatus*) was clearly influenced by the spatial scale considered and increased consistently at larger spatial scales (Fig. 2). For *A. montensis* and *E. russatus*, this increase in power occurred only when considering the matrix as unsuitable, while for *M. paraguayanus*, it was consistent across all metrics of habitat quantity (Fig. 2). On the other hand, the explanatory power of all models of

Table 2. Results from Poisson regressions of the abundance of small mammal species against habitat quantity (considering or not matrix quality and using as indices of matrix quality both species abundance – A or occurrence – O) within circumferences of 200, 400 and 800 m of radius around the 20 forest remnants in the Ibiúna Plateau, Brazil.

Species	Not considering matrix quality						Considering matrix quality					
	scale 200 m		scale 400 m		scale 800 m		scale 200 m		scale 400 m		scale 800 m	
	b (slope)	p	b (slope)	p	b (slope)	p	b (slope)	p	b (slope)	p	b (slope)	p
<i>E. russatus</i>	0.233	0.044*	0.105	<0.001*	0.036	<0.001*	0.071	0.260	0.015	0.320	0.015	0.008
<i>D. aurita</i>	-0.117	0.012*	-0.034	0.015*	-0.011	0.025*	0.081	0.217	0.019	0.230	0.019	0.118
<i>D. sublineatus</i>	0.060	0.313	0.012	0.424	0.007	0.123	0.049	0.229	0.006	0.180	0.006	0.298
<i>M. incanus</i>	0.035	0.348	0.012	0.185	0.003	0.309	0.049	0.229	0.015	0.141	0.004	0.226
<i>S. angouya</i>	-0.012	0.882	-0.002	0.942	0.005	0.452	0.080	0.514	0.017	0.570	0.012	0.228
<i>O. nigripes</i>	-0.050	0.347	-0.015	0.326	-0.003	0.551	0.040	0.658	0.010	0.690	0.008	0.276
<i>A. montensis</i>	-0.013	0.617	-0.017	0.020*	-0.013	<0.001*	1.126	0.555	0.003	0.720	0.005	0.085
<i>M. paraguayanus</i>	0.150	0.377	0.100	0.040*	0.035	0.005*	0.294	0.402	0.062	0.710	0.001	0.233
							0.140	0.434	0.196	0.047*	0.068	0.005*
							0.140	0.434	0.092	0.060	0.033	0.005*

*p < 0.05.

Table 3. Results from Poisson regressions of the abundance of small mammal species against forest connectivity based on the distance and size of forest remnants within a maximum edge-to-edge distance of 50, 100, 200 and 400 m from the 20 forest remnants in the Ibiúna Plateau, Brazil.

Species	Connectivity based on the distance and size of forest patches							
	scale 50 m		scale 100 m		scale 200 m		scale 400 m	
	b (slope)	p	b (slope)	p	b (slope)	p	b (slope)	p
<i>E. russatus</i>	3.077e-04	0.031*	2.977e-04	0.027*	2.978e-04	0.028*	2.970e-04	0.029*
<i>D. aurita</i>	-1.080e-04	0.271	-1.073e-04	0.262	-1.072e-04	0.265	-1.070e-04	0.265
<i>D. sublineatus</i>	-1.628e-04	0.209	-1.544e-04	0.219	-1.547e-04	0.221	-1.548e-04	0.221
<i>M. incanus</i>	9.162e-05	0.145	8.597e-05	0.156	8.281e-05	0.176	8.281e-05	0.176
<i>S. angouya</i>	5.567e-05	0.698	4.559e-05	0.744	5.034e-05	0.719	5.038e-05	0.718
<i>O. nigripes</i>	7.327e-05	0.439	7.720e-05	0.394	7.340e-05	0.423	7.247e-05	0.429
<i>A. montensis</i>	-7.657e-05	0.159	-7.362e-05	0.162	-7.668e-05	0.150	-7.676e-05	0.149
<i>M. paraguayanus</i>	9.274e-04	0.002*	8.786e-04	0.001*	8.814e-04	0.001*	8.809e-04	0.001*

* $p < 0.05$.

habitat connectivity for all eight species was not affected by spatial scale (Fig. 2).

Discussion

Distribution of small mammals in the landscape and habitat quality

Our results indicate that open anthropogenic habitats (rural areas with buildings and areas of agriculture), which correspond to 52.5% of the landscape in Ibiúna, do not harbor populations of the majority of small mammal species found in forest remnants in this region (see also Umetsu and Pardini 2007). Only two species (*A. montensis* and *O. nigripes*) were frequently found in these open habitats, which were widely distributed among forest remnants and occupied all other habitats in the matrix, and can thus be considered highly generalist species. These results are in accordance with previous information suggesting that altered open habitats in fragmented landscapes in the Atlantic forest are dominated by species belonging to these two genera of rodents (Katz et al. 2001, Feliciano et al. 2002).

The other two types of matrix habitats found in Ibiúna (native vegetation in initial stages of regeneration and homogeneous eucalyptus plantation) comprised 14.5% of the landscape and probably harbor populations of some of the small mammal species found in forest remnants, besides the generalist ones. Apparently, these two types of habitats are complementary for increasing landscape connectivity since they harbor different groups of species (Umetsu and Pardini 2007).

Landscape structure variables and the distribution of small mammals in forest remnants

Our results show that, for three of the six native small mammal species that were able to occupy at least one type of matrix, the best models for the distribution among forest remnants were those that considered the heterogeneous quality of the matrix. The importance of considering matrix quality was also stressed in the results of the few published studies that compared the performance of models considering or not matrix heterogeneity, most of which were carried

out in temperate regions. In general, models considering the variation in matrix quality were more adequate to explain species abundance (Lindenmayer et al. 2000), species occurrence (Verbeylen et al. 2003) or inter-patch movements (Ferreras 2001, Sutcliffe et al. 2003, Revilla et al. 2004) than the models that did not consider matrix quality.

In all above mentioned studies, however, matrix heterogeneity was quantified based on the researcher's experience or inferred from auto-ecological studies available in the literature. We did not find published studies evaluating the performance of models that considered matrix quality based on empirical data gathered in a standardized way. Our study shows that it is feasible to obtain indices of matrix quality through standardized sampling in different types of matrix, which may increase the predictive power of landscape structure variables for species distribution and abundance in fragmented landscapes. Contrary to the expectation that abundance could indicate the risk of extinction or the chance of dispersal and thus improve the performance of indices of matrix quality, the index corresponding to species occurrence resulted in similar or higher explanatory power compared to that of species abundance, for all models (species/landscape variables) for which the inclusion of matrix heterogeneity increased model performance. Therefore, the index corresponding to species occurrence seems to be preferable since it depends on data easier to obtain and leads to more rapid biological assessments.

In Ibiúna, however, a consistent increase in explanatory power between models that did or did not consider matrix heterogeneity occurred for the connectivity models, but not for the habitat quantity models. This clearly indicates the importance of taking into account the distance among patches, which is a simple way of representing the chance of dispersal. It is probable that some types of matrix that do not provide a suitable habitat for small mammal species allow periodical dispersal to take place, thus promoting connection among populations in remnants. As Tischendorf et al. (2003) pointed out using simulation models, the metric of connectivity based on the distance and size of patches predicts immigration rates more reliably than other metrics based on inter-patch distances. Goodwin and Fahrig (2002) also showed in simulation models that distance

Table 4. Results from Poisson regressions of the abundance of small mammal species against habitat connectivity based on the distance and size of habitat patches (considering matrix quality and using as indices of matrix quality both species abundance – A or occurrence – O) within a maximum edge-to-edge distance of 50, 100, 200 and 400 m from the 20 forest remnants in the Ibiúna Plateau, Brazil.

Species	Type of index	Connectivity based on the distance and size of habitat patches											
		scale 50 m			scale 100 m			scale 200 m			scale 400 m		
		b (slope)	p	b (slope)	p	b (slope)	p	b (slope)	p	b (slope)	p		
<i>D. sublineatus</i>	A	-1.409e-05	0.671	-1.386e-05	0.672	-1.376e-05	0.675	-1.377e-05	0.675	-5.088e-06	0.778	-5.088e-06	0.778
	O	-5.163e-06	0.776	-5.122e-06	0.777	-5.085e-06	0.778	-5.085e-06	0.778	2.178e-05	0.242	2.178e-05	0.242
<i>M. incanus</i>	A	2.348e-05	0.217	2.242e-05	0.226	2.178e-05	0.243	2.178e-05	0.243	8.147e-06	0.387	8.146e-06	0.387
	O	8.334e-06	0.379	8.237e-06	0.381	8.147e-06	0.387	8.147e-06	0.387	-2.077e-05	0.520	-2.076e-05	0.520
<i>S. angouya</i>	A	-2.090e-05	0.519	-2.091e-05	0.518	-2.091e-05	0.518	-2.091e-05	0.518	-1.853e-05	0.543	-1.851e-05	0.543
	O	-1.866e-05	0.542	-1.869e-05	0.540	-1.869e-05	0.540	-1.869e-05	0.540	2.713e-06	<0.001*	2.713e-06	<0.001*
<i>O. nigripes</i>	A	2.713e-06	<0.001*	2.713e-06	<0.001*	2.713e-06	<0.001*	2.713e-06	<0.001*	4.383e-06	<0.001*	4.383e-06	<0.001*
	O	4.386e-06	<0.001*	4.382e-06	<0.001*	4.383e-06	<0.001*	4.383e-06	<0.001*	4.305e-07	0.116	4.303e-07	0.116
<i>A. montensis</i>	A	4.318e-07	0.115	4.308e-07	0.116	4.308e-07	0.116	4.308e-07	0.116	2.094e-06	<0.001*	2.094e-06	<0.001*
	O	2.097e-06	<0.001*	2.095e-06	<0.001*	2.095e-06	<0.001*	2.095e-06	<0.001*	5.624e-04	<0.001*	5.624e-04	<0.001*
<i>M. paraguayanus</i>	A	5.743e-04	<0.001*	5.621e-04	<0.001*	5.621e-04	<0.001*	5.624e-04	<0.001*	1.674e-04	<0.001*	1.674e-04	<0.001*
	O	1.695e-04	<0.001*	1.674e-04	<0.001*	1.674e-04	<0.001*	1.675e-04	<0.001*				

*p < 0.05.

influenced landscape connectivity metrics more strongly than amount of habitat in artificial landscapes with < 32% of remaining habitat.

For three species that occurred in just one type of matrix (native vegetation in initial stages of regeneration), there was no improvement in explanatory power of models considering distance, matrix quality or different spatial scales in relation to the null model. The fact that initial vegetation was the habitat type that occupied the smallest proportion of cover around the sampled remnants may have contributed to the absence of improvements in the models that included matrix quality for these species. Nevertheless, five (*E. russatus*, *D. aurita*, *M. paraguayanus*, *A. montensis* and *O. nigripes*) out of eight species had their abundance in remnants explained by at least one of the landscape variables and metrics in at least one of the spatial scales used in this study.

It is noteworthy that the habitat quantity models were consistently better than the habitat connectivity models across all spatial scales only for the two small mammal species (*E. russatus* and *D. aurita*) that did not occur in any of the matrix habitats. Among those, the terrestrial forest-dwelling rodent *E. russatus* presented the most consistent relationship with landscape structure, the abundance increasing with the increase in forest quantity and connectivity. This species is the dominant species in small mammal communities in continuous Atlantic forests in southeast Brazil (Pardini and Umetsu 2006), and is the most vulnerable to fragmentation, showing a clear reduction in abundance with the decrease in remnant size (Pardini et al. 2005, Umetsu and Pardini 2007). The common opossum *D. aurita*, on the other hand, although not captured in matrix habitats, increased in abundance in landscape contexts with low proportion of forest and, therefore, of large proportion of altered habitats. *Didelphis aurita* is the species with the largest body size (985 g – Fonseca et al. 1996), largest home range that usually includes several remnants, and widest movements through open areas (Pires et al. 2002) among the studied species. Additionally, this species has a highly omnivorous diet (Fonseca et al. 1996), and frequently uses resources that are associated with human activities, such as refuse and small domesticated animals. These characteristics indicate that the observed negative relationship of *D. aurita* with forest quantity is a consequence of the capacity of individuals to explore and to benefit from surrounding altered habitats, although not populating or living in those habitats, as confirmed by other studies (Feliciano et al. 2002, Pires et al. 2002). For this species, it seems that the correct modeling of the importance of the altered habitats would only be possible through indices of matrix quality that quantify matrix use, not only matrix occupation as we did.

For the three species that occurred in the matrix (*M. paraguayanus*, *A. montensis* and *O. nigripes*), however, the best models to explain their abundance in remnants were the connectivity models, thus including the distance among habitat patches, and considering matrix heterogeneity. *Micoureus paraguayanus* is a relatively rare species in Ibiúna that does not occupy all the habitats in the landscape. Although rare and performed only by males, the dispersal of individuals of this species among remnants of Atlantic forest surrounded by open habitats has been

proven to occur (Quental et al. 2001), indicating that in fact including the distance among habitat patches should increase the explanatory power of landscape models for this marsupial. On the other hand, the rodents *A. montensis* and *O. nigripes* were widely distributed among remnants and commonly found in all habitat types. Our results suggest that, for these generalist species, it is inadequate to consider only forest as habitat. These species seems to be favored by the increase in matrix habitats. Indeed, in Ibiúna the most adequate habitats for *A. montensis* and *O. nigripes* were the altered habitats of the matrix, as shown by their higher abundance in many anthropogenic habitats compared to forest remnants. For these species, only when taking into account the heterogeneity, quantity and distance of matrix habitats it was possible to adequately model their abundance in remnants, stressing the need for classifying and investigating habitat as a species-specific concept, i.e. a range of environments suitable for a given species (Fischer and Lindenmayer 2007). In fact, for *A. montensis*, although the model of habitat quantity considering just forest as habitat at large scales was significant, it led to an opposite relationship to those of habitat connectivity considering matrix quality, i.e. a decrease in abundance as the amount of forest increase, indicating that the species was more abundant in remnants with larger amounts of surrounding altered habitats. The focus of most studies of the effects of landscape structure is mainly on species that are restricted to remnant habitats, while these effects are poorly understood for species that have a more generalist use of habitats (Virgós 2002). Simulation models in Bender and Fahrig (2005) showed that for a generalist species, inter-patch movements are difficult to predict, probably because generalist species interact with a large number of cover types and exhibit different responses to them, when moving among patches. In the present study, we show that it is possible to model the response of generalist species to landscape structure, as far as matrix quality is considered.

Besides the consistency across species in increasing the explanatory power when considering the quality of matrix habitats, connectivity models were also less variable across spatial scales compared to habitat quantity models. This corroborates the findings of Bender et al. (2003) that showed through simulation models that the use of metrics that consider the distance and size of habitat patches present higher explanatory power and vary in a narrower range under different spatial scales. Tischendorf et al. (2003) also found that the fit of these metrics in simulations did not change with varying scales. This property favors the use of these metrics, since establishing appropriate scales for different species is a difficult task and choosing inappropriate scales may lead to failure in the detection of patterns (Vos et al. 2001, Bender et al. 2003).

The only three species for which the responses to habitat quantity varied among spatial scales showed a consistent stronger response with increasing spatial scale. All three species have body sizes that vary from 34 to 124 g (data from this study for *A. montensis* and *M. paraguayanus* and from Fonseca et al. (1996) for *E. russatus*), indicating that landscape structure influences small mammals in relatively large spatial scales, despite their small body size and restricted movements.

The results set forth here show that simple and easily obtainable indices of matrix quality increase the predictive power of landscape structure variables if distance, a simple estimate of the chance of dispersal among patches, is taken into account. This is specially the case for species with generalist habits that are able to occupy different habitat types. This indicates that the matrix of altered habitats not only plays a fundamental role in ecological processes, but also could be taken into account for modeling, monitoring and managing human-dominated landscapes, even if accurate and detailed information on the biology of species is not available. The use of indices based on species abundance or occurrence may contribute to the understanding of the importance of matrix quality, enabling effective management actions in fragmented tropical landscapes. Among landscape structure variables, those that incorporate size, species-specific habitat quality, and distance among habitat patches are preferable, since they were not only efficient to explain the abundance of a greater number of species, but also less variable across spatial scales. The few consistent responses to the variation in spatial scale indicate that despite their small size and short daily movements, small mammal distribution in forest remnants is influenced by landscape structure at relatively large spatial scales, probably reflecting population processes over long time periods.

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References

- Antongiovanni, M. and Metzger, J. P. 2005. Influence of matrix habitats on the occurrence of insectivorous bird species in Amazonian forest fragments. – *Biol. Conserv.* 122: 441–451.
- Bender, D. J. and Fahrig, L. 2005. Matrix structure obscures the relationship between interpatch movement and patch size and isolation. – *Ecology* 86: 1023–1033.
- Bender, D. J. et al. 2003. Using patch isolation metrics to predict animal movement in binary landscapes. – *Landscape Ecol.* 18: 17–39.
- Bergallo, H. G. 1994. Ecology of small mammal community in an Atlantic forest area in southeastern Brazil. – *Stud. Neotrop. Fauna Environ.* 29: 197–217.
- Bergallo, H. G. 1995. Comparative life-history characteristics of two species of rats, *Proechimys iheringi* and *Oryzomys intermedius*, in an Atlantic forest of Brazil. – *Mammalia* 59: 51–64.
- Bergallo, H. G. and Magnusson, W. E. 2004. Factors affecting the use of space by two rodent species in Brazilian Atlantic forest. – *Mammalia* 68: 121–132.
- Bowman, J. et al. 2001. The spatial component of variation in small-mammal abundance measured at three scales. – *Can. J. Zool.* 79: 137–144.

- Bowman, J. et al. 2002. Dispersal distance of mammals is proportional to home range size. – *Ecology* 83: 2049–2055.
- Brewer, S. W. and Rejmanek, M. 1999. Small rodents as significant dispersers of tree seeds in a Neotropical forest. – *J. Veg. Sci.* 10: 165–174.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.
- Castro, E. B. V. and Fernandez, F. A. S. 2004. Determinants of differential extinction vulnerabilities of small mammals in Atlantic forest fragments in Brazil. – *Biol. Conserv.* 119: 73–80.
- Costa, L. P. et al. 2005. Mammal conservation in Brazil. – *Conserv. Biol.* 19: 672–679.
- Daily, G. C. et al. 2003. Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. – *Conserv. Biol.* 17: 1814–1826.
- Debinski, D. M. and Holt, R. 2000. A survey and overview of habitat fragmentation experiments. – *Conserv. Biol.* 14: 342–355.
- DeFries, R. et al. 2005. Increasing isolation of protected areas in tropical forests over the past twenty years. – *Ecol. Appl.* 15: 19–26.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. – *Annu. Rev. Ecol. Evol. Syst.* 34: 487–515.
- Feliciano, B. R. et al. 2002. Population dynamics of small rodents in a grassland between fragments of Atlantic forest in southeastern Brazil. – *Mamm. Biol.* 67: 304–314.
- Ferreras, P. 2001. Landscape structure and asymmetrical interpatch connectivity in a metapopulation of the endangered Iberian lynx. – *Biol. Conserv.* 100: 125–136.
- Fischer, J. and Lindenmayer, D. B. 2007. Landscape modification and habitat fragmentation: a synthesis. – *Global Ecol. Biogeogr.* 16: 265–280.
- Fonseca, G. A. et al. 1996. Lista anotada dos mamíferos do Brasil. – *Occas. Pap. Conserv. Biol.* 4: 1–38.
- Gardner, R. H. and Gustafson, E. J. 2004. Simulating dispersal of reintroduced species within heterogeneous landscapes. – *Ecol. Model.* 171: 339–358.
- Gascon, C. et al. 1999. Matrix habitat and species richness in tropical forest remnants. – *Biol. Conserv.* 91: 223–229.
- Gentile, R. and Cerqueira, R. 1995. Movement patterns of five species of small mammals in a Brazilian restinga. – *J. Trop. Ecol.* 11: 671–677.
- Gobeil, J. and Villard, M. 2002. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. – *Oikos* 98: 447–458.
- Goodwin, B. J. and Fahrig, L. 2002. How does landscape structure influence landscape connectivity? – *Oikos* 99: 552–570.
- Haila, Y. 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. – *Ecol. Appl.* 12: 321–334.
- Hilborn, R. and Mangel, M. 1997. The ecological detective: confronting models with data. – Princeton Univ. Press.
- Jules, E. and Shahani, P. 2003. A broader ecological context to habitat fragmentation: why matrix habitat is more important than we thought. – *J. Veg. Sci.* 14: 459–464.
- Katz, G. et al. 2001. Hantavirus pulmonary syndrome in the State of São Paulo, Brazil, 1993–1998. – *Vector Borne Zoonotic Disease* 1: 181–190.
- Kupfer, J. A. et al. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. – *Global Ecol. Biogeogr.* 15: 8–20.
- Lambert, T. D. et al. 2006. Amazonian small mammal abundances in relation to habitat structure and resource abundance. – *J. Mammal.* 87: 766–776.
- Lindenmayer, D. B. et al. 2000. Testing a simulation model for population viability analysis. – *Ecol. Appl.* 10: 580–597.
- McGarigal, K. and Marks, B. J. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. – USDA Forest Service General Technical Report PNW-351, <<http://www.umass.edu/landeco/pubs/pubs.html#fragstats>>.
- Metzger, J. P. 2000. Tree functional group richness and landscape structure in a Brazilian tropical fragmented landscape. – *Ecol. Appl.* 10: 1147–1161.
- Moilanen, A. and Nieminen, M. 2002. Simple connectivity measures in spatial ecology. – *Ecology* 83: 1131–1145.
- Oliveira-Filho, A. T. and Fontes, M. A. L. 2000. Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. – *Biotropica* 32: 793–810.
- Oliveira Filho, F. J. B. and Metzger, J. P. 2006. Thresholds in landscape structure for three common deforestation patterns in the Brazilian Amazon. – *Landscape Ecol.* 21: 1061–1073.
- Pardini, R. 2004. Effects of forest fragmentation on small mammals in an Atlantic forest landscape. – *Biodiv. Conserv.* 13: 2567–2586.
- Pardini, R. and Umetsu, F. 2006. Pequenos mamíferos não-voadores da Reserva Florestal do Morro Grande – distribuição das espécies e da diversidade em uma área de Mata Atlântica. – *Biota Neotropica* 6, <<http://www.biotaneotropica.org.br/v6n2/pt/abstract?article+bn01006022006>>.
- Pardini, R. et al. 2005. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. – *Biol. Conserv.* 124: 253–266.
- Perfecto, I. and Vandermeer, J. 2002. Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. – *Conserv. Biol.* 16: 174–182.
- Pires, A. S. et al. 2002. Frequency of movements of small mammals among Atlantic forest fragments in Brazil. – *Biol. Conserv.* 108: 229–237.
- Quental, T. B. et al. 2001. Population dynamics of the marsupial *Micoureus demerarae* in small fragments of Atlantic coastal forest in Brazil. – *J. Trop. Ecol.* 17: 339–352.
- R Development Core Team 2006. R: a language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org>.
- Revilla, E. et al. 2004. Effects of matrix heterogeneity on animal dispersal: from individual behavior to metapopulation-level parameters. – *Am. Nat.* 164: 130–153.
- Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. – *Am. Nat.* 158: 87–99.
- Ross, J. L. S. and Moroz, I. C. 1997. Mapa geomorfológico do Estado de São Paulo: escala 1:500.000. – FFLCH-USP, IPT and FAPESP.
- Royall, R. 2004. The likelihood paradigm for statistical evidence. – In: Taper, M. L. and Lele, S. R. (eds), *The nature of scientific evidence: statistical, philosophical, and empirical considerations*. Univ. of Chicago Press, pp. 119–152.
- Schooley, R. L. and Wiens, J. A. 2004. Movements of cactus bugs: patch transfers, matrix resistance, and edge permeability. – *Landscape Ecol.* 19: 801–810.
- Silva, W. G. et al. 2007. Relief influence on the spatial distribution of the Atlantic forest cover at the Ibiúna Plateau, SP. – *Braz. J. Biol.* 67: 631–637.
- Soares-Filho, B. et al. 2006. Modeling conservation in the Amazon basin. – *Nature* 440: 520–523.
- Steffan-Dewenter, I. et al. 2002. Scale-dependent effects of landscape context on three pollinator guilds. – *Ecology* 83: 1421–1432.
- Stevens, V. M. et al. 2004. Quantifying functional connectivity: experimental evidence for patch-specific resistance in the natterjack toad (*Bufo calamita*). – *Landscape Ecol.* 19: 829–842.

- Sutcliffe, O. L. et al. 2003. Modelling the benefits of farmland restoration: methodology and application to butterfly movement. – *Landscape Urban Plann.* 63: 15–31.
- Tabarelli, M. et al. 2005. Challenges and opportunities for biodiversity conservation in the Brazilian Atlantic forest. – *Conserv. Biol.* 19: 695–700.
- Tischendorf, L. and Fahrig, L. 2000. On the usage and measurement of landscape connectivity. – *Oikos* 90: 7–19.
- Tischendorf, L. et al. 2003. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. – *Landscape Ecol.* 18: 41–50.
- Umetsu, F. and Pardini, R. 2007. Small mammals in a mosaic of forest remnants and anthropogenic habitats – evaluating matrix quality in an Atlantic forest landscape. – *Landscape Ecol.* 22: 517–530.
- Umetsu, F. et al. 2006. Evaluating the efficiency of pitfall traps for sampling small mammals in the Neotropics. – *J. Mammal.* 87: 757–765.
- Vandermeer, J. and Carvajal, C. 2001. Metapopulation dynamics and the quality of the matrix. – *Am. Nat.* 158: 211–220.
- Verbeylen, G. et al. 2003. Does matrix resistance influence red squirrel (*Sciurus vulgaris* L. 1758) distribution in an urban landscape? – *Landscape Ecol.* 18: 791–805.
- Virgós, E. 2002. Are habitat generalists affected by forest fragmentation? A test with Eurasian badgers (*Meles meles*) in coarse-grained fragmented landscapes of central Spain. – *J. Zool.* 258: 313–318.
- Vos, C. C. et al. 2001. Toward ecologically scaled landscape indices. – *Am. Nat.* 183: 24–41.
- Wijesinghe, M. R. and Brooke, M. D. 2005. Impact of habitat disturbance on the distribution of endemic species of small mammals and birds in a tropical rain forest in Sri Lanka. – *J. Trop. Ecol.* 21: 661–668.
- Winfree, R. et al. 2005. Testing simple indices of habitat proximity. – *Am. Nat.* 165: 107–117.