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Immigration Rates in Fragmented Landscapes – Empirical Evidence for the Importance of Habitat Amount for Species Persistence

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Abstract

Background: The total amount of native vegetation is an important property of fragmented landscapes and is known to exert a strong influence on population and metapopulation dynamics. As the relationship between habitat loss and local patch and gap characteristics is strongly non-linear, theoretical models predict that immigration rates should decrease dramatically at low levels of remaining native vegetation cover, leading to patch-area effects and the existence of species extinction thresholds across fragmented landscapes with different proportions of remaining native vegetation. Although empirical patterns of species distribution and richness give support to these models, direct measurements of immigration rates across fragmented landscapes are still lacking.

Methodology/Principal Findings: Using the Brazilian Atlantic forest marsupial Gray Slender Mouse Opossum (*Marmosops incanus*) as a model species and estimating demographic parameters of populations in patches situated in three landscapes differing in the total amount of remaining forest, we tested the hypotheses that patch-area effects on population density are apparent only at intermediate levels of forest cover, and that immigration rates into forest patches are defined primarily by landscape context surrounding patches. As expected, we observed a positive patch-area effect on *M. incanus* density only within the landscape with intermediate forest cover. Density was independent of patch size in the most forested landscape and the species was absent from the most deforested landscape. Specifically, the mean estimated numbers of immigrants into small patches were lower in the landscape with intermediate forest cover compared to the most forested landscape.

Conclusions/Significance: Our results reveal the crucial importance of the total amount of remaining native vegetation for species persistence in fragmented landscapes, and specifically as to the role of variable immigration rates in providing the underlying mechanism that drives both patch-area effects and species extinction thresholds.

Introduction

The effects of patch size and isolation on populations have been intensively investigated, providing empirical evidence of their influence on demographic parameters, such as population size [1,2], survival rates [3–5], and extinction probabilities [2,6]. However, studies are usually conducted in single landscapes, despite the growing recognition that population dynamics in patches cannot be considered in isolation of the wider landscape context [7,8].

Among whole-landscape properties, the total amount of remaining native vegetation (i.e. the amount of original, naturally occurring vegetation type) is expected to be of particular importance to populations in patches due to its non-linear relationships to patch- as well as gap-characteristics [9–12]. Simulation models suggest that the number of patches as well as the total amount of edge habitat is highest in landscapes with intermediate native vegetation cover, while the size of the largest patch decreases dramatically at around 60% habitat cover [9,11]. By contrast, gap characteristics such as the average distances among neighboring patches increase exponentially below ~10–20% habitat cover [9,11] and therefore should have a strong influence on patterns of dispersal [13–15], increasing population isolation and decreasing the probability of rescue effects [16]. Small population sizes coupled with limited dispersal can increase vulnerability to local extinctions [17] and ultimately increase

extinction probabilities at the landscape scale (i.e. species extinction thresholds; [13,18–20]).

In linking the interaction between landscape context with patch-area effects, Andrén [9] and more recently Pardini *et al.* [20] proposed theoretical models that include a threshold in the total amount of remaining native vegetation, below which a positive patch-area effect on population density becomes apparent due to the increased isolation of patches. In this model the isolation of patches and consequent changes in immigration rates are defined by the total amount of native vegetation at the landscape scale [20]. According to the model, a moderate reduction in habitat cover should only affect populations in small patches, which due to their small size are more dependent on immigration to ensure population persistence, leading to a patch-area effect [9,20]. By contrast a high level of vegetation clearance drives an exponential increase in distances among patches [10], leading to a drastic reduction in immigration rates and an increase in extinction risk within even the largest remaining patches [20].

Following a detailed review of available literature, Andrén [9] found evidence for patch-area effects only in studies carried out in landscapes with ≤ 30% of remaining native vegetation. In the first targeted empirical test of this theoretical model, Pardini *et al.* [20] found evidence for patch-area effects on the richness and total abundance of the assemblage of habitat specialist small mammals only in a landscape characterized by intermediate levels of native vegetation cover (30%). Where vegetation clearance was high (10% native vegetation cover), an abrupt drop in landscape-wide richness and no evidence for patch-area effects on this assemblage was observed. However, despite this empirical support, direct evidence of reduced immigration into patches in landscapes with decreasing amounts of native vegetation – the principal mechanism driving patch-effects in the Andrén-Pardini model – is lacking [20].

In this study, we combine pattern and process orientated research approaches to investigate the demographic processes behind patterns of species abundance and persistence in patches in different landscape contexts [8,21,22]. We investigated patterns of population density and estimated demographic parameters of the endemic Gray Slender Mouse Opossum *Marmosops incanus* (Lund 1840, Didelphidae) in patches located in three 10000-ha Brazilian Atlantic forest landscapes which are characterized by different amounts of remaining forest (50, 30, and 10%). *M. incanus* is a small marsupial species (adult weight: 22 to 60 g in the study area; Barros, *unpublished data*) with a seasonal reproduction pattern (reproduction in the rainy season [23,24]), peaks in abundances between December and June, and without strong inter-annual variation in abundance in the study area (Barros, *unpublished data*). It is a forest specialist species showing high habitat [25] as well as micro-habitat specificity [26], while also being relatively common and therefore amenable to population parameter estimation. Using two different data sets, we tested the hypotheses that: (1) patch-area effects on population density are apparent only at an intermediate level of forest cover, below which the species become extinct at the landscape scale (i.e. changes in population density of the model species are consistent with patterns of diversity observed for the assemblage of habitat specialist small mammals in the same landscapes [20]), and (2) immigration rates into patches are defined by landscape context, being higher in patches of the most forested landscape.

Materials and Methods

Study area

Small mammals were sampled in three 10000-ha fragmented landscapes located in the Atlantic Plateau of São Paulo, Brazil, in the municipalities of Tapiraí - Piedade, Ibiúna, and Ribeirão Grande - Capão Bonito (Fig. 1). The entire region was originally covered with Atlantic Forest classified as ''Lower Montane Atlantic Rain Forest'' [27], which is currently reduced to patches of different sizes. In all three landscapes, patches consist of secondary forest and are surrounded mainly by pasture (48%, 44% and 50% of non-forest areas for Tapiraí - Piedade, Ibiúna, and Ribeirão Grande - Capão Bonito, respectively) and agriculture (26%, 20% and 35% of non-forest areas for Tapiraí - Piedade, Ibiúna e Ribeirão Grande - Capão Bonito, respectively). Altitudes are between 800 and 1000 m above sea level [28]. Annual rainfall is between 1222 and 1810 mm and mean minimum and maximum temperatures are 17.3°C and 28.4°C for the warm-wet season (October to March) and 12.1°C and 24.9°C for the cool-dry season (April to September). The three landscapes are similar in terms of topography, relief, climate, and type of human occupation, but vary in the proportion of remaining forest cover from 49% in Tapiraí – Piedade (hereafter referred to as 50%), to 31% in Ibiúna (hereafter 30%) and 11% in Ribeirão Grande - Capão Bonito (hereafter 10%, Fig. 1) and thus in patch and gap characteristics. The landscape with 50% forest cover has the highest percentage of the landscape covered by the largest patch, highest mean patch size, and lowest mean distance to the nearest patch, whereas the landscape with 10% forest cover presents the lowest values for these variables [20].

Sampling design and Data Collection

Ethics Statement. Trapping and handling were approved by IBAMA – Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (permissions 57/02 - IBAMA/SP, 11/04 - IBAMA/SP, 168/2004 - CGFAU/LIC, 237/2005 - CGFAU/LIC, 262/2006 – COFAN, 11577-2 - IBAMA/SP, and 11577-4 - IBAMA/SP) and conformed to guidelines sanctioned by the American Society of Mammalogists Animal Care and Use Committee. Because our study involved only the capture, handling for marking and the immediate release of a small marsupial in the field, it did not receive an approval from the Ethics Committee of the Institute of Biosciences - University of São Paulo (Comissão de Ética em Uso de Animais Vertebrados em Experimentação– CEA - http://ib.usp.br/etica_animais.htm), which only requires approval for studies on vertebrates that include experimentation (e.g. maintenance in captivity, injection of drugs, or surgery).

Patch-area effect on population density. We sampled 50 forest patches, 15 of which (3 to 145 ha) were located in the landscape with 50% forest cover, 20 in the landscape with 30% (2 to 374 ha) and 15 in the landscape with 10% (6 to 106 ha, Fig. 1). Surveyed forest patches were selected in order to ensure: similar vegetation structure and age (all patches consisted of secondary vegetation in intermediate stages of regeneration and were not subjected to disturbances such as fire, selective logging or cattle), extensive overlap in patch size among landscapes, guarantee a minimum distance among patches, avoid spatial segregation among similar-sized patches, and guarantee a minimum distance of the sampling site from the forest edge (30 m in small fragments but usually more than 50 m). Distances of sites to patch-edge, average distance to the nearest surveyed patch, as well as size and shape of surveyed patches did not differ significantly among landscapes [20]. The percentage of forest cover in an 800 m circumference around sampling sites within surveyed forest patches varied among landscapes (from 22 to 64% in the landscape with 50% of forest cover, 11 to 77% in the landscape with 30%, and 5 to 41% in the landscape with 10%), but was highly correlated with patch size in all three landscapes,
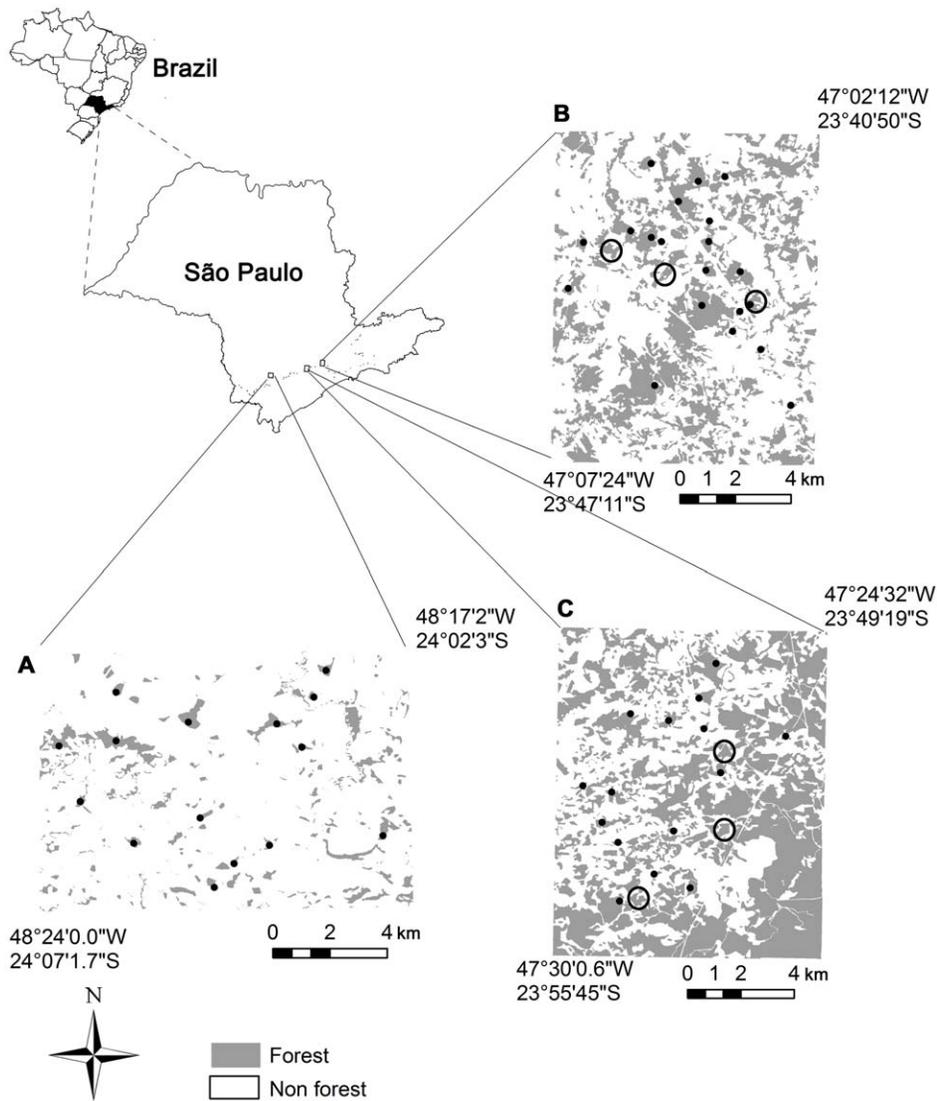
Figure 1. Distribution of forest patches in three fragmented landscapes in the Atlantic Plateau of São Paulo. (A) Fragmented landscape in Ribeirão Grande - Capão Bonito (10% forest cover), (B) fragmented landscape in Ibiúna (30% forest cover) and (C) fragmented landscape in Tapiraí - Piedade (50% forest cover). Forest patches are shown in gray. Dots: patches where *M. incanus* density was quantified (first dataset); circles: small patches where capture-recapture data was collected to estimate demographic parameters (second dataset).
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with larger patches being surrounded by higher amounts of forest [20].

A standardized sampling protocol was used in all 50 sites. The protocol consisted of one 100-m long line of 11 60-L pitfall traps per site, with pitfall traps located 10 m from each other and connected by a 50-cm high plastic drift-fence. Four 8-day capture sessions were carried out at each site, two in each of two consecutive summers. In the Ibiúna landscape, capture sessions were conducted during the summers of 2001–2002 and 2002–2003, and in the other two landscapes during the summers of 2005–2006 and 2006–2007. There is no evidence that climatic conditions in the study region varied during the time of the study [29]. Sampling effort was concentrated in the wet season, since daily capture success with pitfall traps is higher at this time of the year [30]. Animals were marked with numbered tags on their first capture (Fish and small animal tag-size 1 – National Band and Tag Co., Newport, Kentucky). The number of individuals of *M. incanus* captured in the standardized area

sampled in each of the 50 surveyed patches was used as an index of population density (hereafter density) and represents the first dataset.

Effect of landscape forest cover on immigration rates. Population demography was investigated in three small forest patches in each of the two most forested landscapes (50 and 30% forest cover), since the focus species was absent from the most deforested landscape (see results from the first data set). Patches were chosen to guarantee consistent differences in the amount of surrounding forest between landscapes, but to be otherwise similar (Fig. 1; Fig. S1):

(1) similar size (30% landscape: 19.7 ha, 13.9 ha, 16.9 ha; 50% landscape: 18.3 ha, 14.8 ha, 17.1 ha);

(2) similar distance among surveyed patches in each landscape (Fig. 1; Fig. S1);

(3) similar number of connections to other patches by corridors (Fig. 1; Fig. S1);

(4) similar forest structure (all patches are comprised of secondary forest in intermediate stage of regeneration);

(5) different percentage of surrounding forest cover in order to maintain the overall percentage in the respective landscape (calculated in three radii around the center of each patch; 30% landscape 1 km: $28.7\% \pm 0.03$; 1.5 km: $30.4\% \pm 0.03$; 2 km: $30.6\% \pm 0.03$; 50% landscape 1 km: $52.4\% \pm 0.07$, 1.5 km: $51.0\% \pm 0.01$, 2 km: $48.1\% \pm 0.03$; all values mean among patches $\pm$ SD; Fig. S1).

A trapping grid of 2 ha was placed in each of the six patches (Fig. S2). Given the irregular shape of patches, one side of the grid was near to a forest edge in each of the six surveyed patches. Each grid consisted of 11 parallel 100-m long lines, 20 m from each other, with 11 trapping stations spaced every 10 m. In each trapping station one Sherman trap (size: 37.5 x 10.0 x 12.0 cm or 23.0 x 7.5 x 8.5 cm) was placed on the ground. In addition, five lines were also equipped with one 60-L pitfall trap per station, connected to each other by a 50-cm high plastic fence (similar to the trapping lines used for the investigation of patch-area effect on density). Two different trap types were used to maximize both capture and recapture rates, since pitfall traps result in higher capture rate and higher proportion of young individuals, while recapture rates are higher in Sherman traps [30]. All traps were baited with a mixture of sardines, peanut butter, banana, and manioc flour. Precautions were taken to minimize mortality in pitfall traps (bucket lids were used as a roof protecting from rain, small holes in the bottom facilitated drainage, and a styrofoam disc provided a dry surface in the event of accumulation of water).

Trapping design followed Pollock's robust design [31,32], with short primary capture sessions assuming population closure, separated by relatively longer time periods, thereby allowing for open population processes. Animals were captured during five 5-day primary capture sessions with a 20-day interval between them, resulting in 26400 trap nights in total. This protocol was carefully established from our field experience with Atlantic forest small mammals, for which between-primary session recaptures tend to be very low due to short life-cycles. It represents a trade-off between guaranteeing open population processes between primary sessions on the one hand, and maximizing between-primary session recapture probabilities, which are a crucial requirement for the precise estimation of population parameters [33], on the other. Trapping within each primary session was carried out simultaneously in the three grids of each landscape, and consecutively (with no interval) between landscapes, to minimize the influence of weather and season on results and guarantee comparable estimates between landscapes. All five primary capture sessions were carried out between February and June of 2008. Captured animals were weighed, sexed, and marked with a numbered ear tag (small animal tags OLT – A. Hartenstein GmbH, Würzburg/Versbach, Germany) and released in the respective trapping location. The capture histories of *M. incanus* represent the second dataset used in the analyses.

Data analyses

Patch-area effect on population density. The data on the density of *M. incanus* in the 50 patches of the three fragmented landscapes was confronted with eight alternative models (Fig. 2), which were compared using an information-theoretic model selection approach [34]. Each candidate model is a combination of linear and/or constant functions, and corresponds to either (1) the lack of relationship between density and patch area or landscape context, (2) a positive relationship with patch area independent of landscape context, (3) a relationship with landscape context independent of patch area, or (4) a positive relationship with patch area in one, two, or three landscapes depending on landscape context (Fig. 2).

The log-likelihood of each model was calculated as the sum of the log-likelihoods of their component functions, with the maximum likelihood estimates for coefficients being the set of values that minimized the whole model negative log-likelihood (i.e. the sum of the negative log-likelihood of the component functions). As usual for count data, all models were fitted using log as the link function. Density was modeled as a Poisson variable in models with patch-area effect, and as a negative binomial variable in constant functions (i.e. without patch-area effects) due to high variance in these cases. Patch areas were converted by their logarithms (base 10). The Akaike Information Criterion corrected for small samples (AIC_c) was calculated for each model and the plausibility of alternative models was estimated by the differences in their AIC_c values in relation to the AIC_c of the most plausible model (Δ_i), where a value of $\Delta_i \leq 2$ indicates equally plausible models. All analyses were conducted in the R environment, version 2.13.0 [35].

Effect of landscape forest cover on immigration rates. To estimate the number of immigrants in each forest patch in each primary capture session, we first used capture-recapture histories of *M. incanus* to estimate abundance, apparent survival rates (including survival and emigration rates; hereafter survival rate) and population rates of change in program MARK version 6.0 [36]. Testing for population closure within primary capture sessions was performed with the program CloseTest (Stanley and Richards, Fort Collins Science Center, http://www.mesc.usgs.gov/Products/Software/closetest/) using Stanley and Burnham test for closure [37] when possible (in 24 of 30 primary capture sessions). Because only in five out of 24 primary capture sessions tests indicated violation of closure ($\chi^2 > 5.15$; $p < 0.05$), and the number of trapping days per primary capture session was small (5 days), we assumed population closure within primary capture sessions.

Modeling of survival rates and population rates of change was based on Pollock's robust design models [31,32] and Pradel Lambda models [38]. To assess whether survival rates (φ) and population rates of change (λ) of populations of *M. incanus* differ between landscape contexts or forest patches, we considered a set of nine candidate models, among which survival rate and population rate of change were either (1) constant between all patches independent of landscape context, (2) dependent on landscape context, or (3) different between patches independent of landscape context (Table 1):

Model I1 – Survival rate and population rate of change are constant between all patches independent of landscape context: this model represents a null hypothesis of no effects on *M. incanus* demographic parameters;

Model I2 – Survival rate and population rate of change depend on landscape context: the expected values of survival rate and population rate of change are similar within landscapes, but different between them;

Models I3 and I4 – Survival rate depends on landscape context and population rate of change is constant between all patches independent of landscape context (or vice versa): these models assume that the expected values of survival rate are similar within a landscape but different between them, while population rate of change is constant between patches independent of landscape context (Model I3) or vice versa (Model I4);

Models I5 and I6 – Survival rate differs between patches, and population rate of change depends on landscape context (or vice versa): these models assume that the expected values of survival
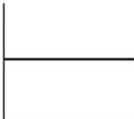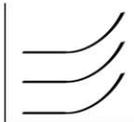
Model		Sketch	K	AIC$_c$	Δ_i	ω_i
D1	Null hypothesis of no patch-area or landscape-context effect: the expected value of *M. incanus* density is a constant		2	304.0	75.2	<0.001
D2	Simple patch-area effect: the expected values of *M. incanus* density are a function of patch area independent from landscape context		2	528.4	299.6	<0.001
D3	Simple landscape-context effect: the expected values of *M. incanus* density are constants that vary among the three landscapes		4	233.1	4.3	0.048
D4	Patch-area and landscape-context effects: the expected values of *M. incanus* density are a function of patch area in each landscape (with similar slopes)		4	272.1	43.3	<0.001
D5	Patch-area and landscape-context effects: the expected values of *M. incanus* density are a function of patch area in each landscape (with different slopes)		6	276.2	47.3	<0.001
D6	Landscape-dependent patch area effect: the expected values of *M. incanus* density are constant in the landscape with 50% forest cover, but a function of patch area in the other two landscapes (similar slopes)		**5**	**228.8**	**0**	**0.418**
D7	Landscape-dependent patch area effect: the expected values of *M. incanus* density are constant in the landscape with 50% forest cover, but a function of patch area in the other two landscapes (different slopes)		6	231.4	2.6	0.115
D8	Landscape-dependent patch-area effect: the expected values of *M. incanus* density are constant in the landscape with 50% and 10% forest cover, but a function of patch area in the landscape with 30% forest cover		**5**	**228.8**	**0**	**0.418**

Figure 2. Set of candidate models to describe the variation in *M. incanus* density. Sketches represent the graphical description of model expectations on density of *M. incanus*. Y-axis: density, either representing a prediction independent of landscape context (single line, Models D1 and D2) or dependent on landscape context (three lines, Models D3 to D8); X-axis: patch area; K is the number of parameters in the model; AIC$_c$ is the modified Akaike information criterion for small sample sizes; Δ_i is the difference between the AIC$_c$ value of model D$_i$ and the AIC$_c$ value of the most parsimonious model; ω_i is the Akaike weight of model D$_i$. Selected models (Models D6 and D8) with lowest AIC$_c$ are shown in bold.
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rate differ between patches independent of landscape context, while population rates of change are similar within a landscape but different between them (Model I5) or vice versa (Model I6);

Models I7 and I8 – Survival rate differs between patches independent of landscape context and population rate of change is constant between patches (or vice-versa): these models assume that the expected values of survival rate and population rate of change are both independent of landscape context, but the values of survival rate depend on patches and those of population rate of change are constant (Model I7) or vice versa (Model I8);

Table 1. Models describing survival rates, population rates of change, capture rates and recapture rates of populations of *M. incanus* in two Atlantic forest landscapes with differing proportions of remaining forest (50% and 30%) in the Atlantic Plateau of São Paulo.

Model				K	AIC$_c$	Δ_i	ω_i	Dev
I2	$\varphi_{(ls)}$	$\lambda_{(ls)}$	$p_{(pa+t)}$	$c_{(pa+t)}$	24	1211.5	0.0	0.377	1157.8
I1	$\varphi_{(.)}$	$\lambda_{(.)}$	$p_{(pa+t)}$	$c_{(pa+t)}$	22	1212.4	0.9	0.234	1163.7
I3	$\varphi_{(ls)}$	$\lambda_{(.)}$	$p_{(pa+t)}$	$c_{(pa+t)}$	23	1212.5	1.0	0.225	1161.4
I4	$\varphi_{(.)}$	$\lambda_{(ls)}$	$p_{(pa+t)}$	$c_{(pa+t)}$	23	1213.6	2.1	0.126	1162.5
I5	$\varphi_{(pa)}$	$\lambda_{(ls)}$	$p_{(pa+t)}$	$c_{(pa+t)}$	28	1218.1	6.6	0.013	1154.4
I6	$\varphi_{(ls)}$	$\lambda_{(pa)}$	$p_{(pa+t)}$	$c_{(pa+t)}$	28	1218.7	7.2	0.010	1155.0
I7	$\varphi_{(pa)}$	$\lambda_{(.)}$	$p_{(pa+t)}$	$c_{(pa+t)}$	27	1218.8	7.3	0.010	1157.6
I8	$\varphi_{(.)}$	$\lambda_{(pa)}$	$p_{(pa+t)}$	$c_{(pa+t)}$	27	1220.9	9.4	0.003	1159.7
I9	$\varphi_{(pa)}$	$\lambda_{(pa)}$	$p_{(pa+t)}$	$c_{(pa+t)}$	32	1224.1	12.6	<0.001	1149.8

In all models, capture rate (p) and recapture rate (c) are specific to the patch (pa) and the primary capture session (t). Survival (φ) and population rate of change (λ) are either considered constant (.), landscape-specific (ls), or patch-specific (pa). K is the number of parameters in the model; AIC$_c$ is the modified Akaike information criterion for small sample sizes; Δ_i is the difference between the AIC$_c$ value of Model I$_i$ and the AIC$_c$ value of the most parsimonious model; ω_i is the Akaike weight of Model I$_i$; Dev is the deviance. Models are ranked by their AIC$_c$-values.
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Model I9 – Survival rate and population rate of change differ between patches independent of landscape context: this model assumes that the expected values of survival rate and population rate of change are both independent of landscape context, but differ between patches.

Based on experience during field work, capture probability (p) and recapture probability (c) were considered different between patches and dependent on primary capture sessions, while constant within primary capture sessions in all candidate models. Because our dataset did not allow for heavily parameterized models, the estimation of population size (N) was conditioned out of the likelihood using Huggins'-closed-capture models within primary capture sessions [39]. We used the logit-link function for estimation of survival, capture, and recapture rates. A log-link function was used for the estimation of population rate of change. Model selection procedure with the Akaike Information Criterion corrected for small samples (AIC$_c$) was the same as described above for the models describing population density. In order to account for model selection uncertainty, we used the AIC$_c$ weights (ω_i) to calculate weighted averages [34,40] of population sizes and survival rates, which were used in the estimation of number of immigrants per capture session.

For the estimation of the number of immigrants per capture session, the estimated number of surviving individuals from the preceding capture session was subtracted from the estimated population size of adults (i.e. estimated population size without young individuals considered to be born in the trapping area and therefore not immigrated) in sessions two to five [41]:

$$\text{Immigrants}_{t+1} = N_{t+1(adult)} - N_t * \phi_t$$

With $N_{t+1(adult)}$: estimated population size of adults at time t+1
N_t: estimated total population size at time t
ϕ_t: estimated survival rate between t and t+1

Model averaged estimates of total population size (N_t) and survival (ϕ_t) were obtained by using the complete capture histories of *M. incanus* for parameter estimation in program MARK. Model averaged estimates of population size of adults ($N_{t+1(adult)}$) were obtained by using reduced capture histories of *M. incanus* excluding young individuals which were considered born in the trapping area and therefore not immigrated. Identification of young individuals was based on tooth eruption patterns [42]. Individuals with up to the second molar erupted in the upper jaw were classified as young individuals, since individuals with the third molar erupted are considered sexually active and therefore potentially moving longer distances [42]. The numbers of immigrants per primary capture session were compared between landscapes using mixed-effect models to control for dependence among primary trapping sessions in the same forest patch (fixed factor: landscape; random factors: forest patch and primary trapping session). The significance of difference between landscapes was verified by Markov chain Monte Carlo simulation (n = 10,000). Statistical analyses were conducted in the R environment, version 2.13.0 [35].

Results

Patch-area effect on POPULATION density

We captured 189 individuals of *M. incanus* distributed across the 15 patches of the 50% landscape, and 178 individuals distributed in 19 out of 20 patches of the 30% landscape, while no individuals were captured in the surveyed patches of the 10% landscape. It is important to note that *M. incanus* was captured in continuously-forested areas adjacent to each of the three fragmented landscapes [20], indicating that its absence in the 10% landscape is not due to biogeographical differences among landscapes. Mean density among surveyed patches was 12.9±9.6 in the 50% landscape and 8.9±4.8 in the 30% landscape (mean ± SD, respectively).

Two models were selected as equally plausible to explain the variation in *M. incanus* density (Model D6 and Model D8, Fig. 2). Both predicted a landscape-dependent patch-area effect only in the landscape with intermediate forest cover (Model D8, Fig. 3) or in the two most deforested landscapes (Model D6). However, in this case Model D6 is redundant with Model D8, since the estimated positive slope coefficient of the patch-area effect on density in the 10% landscape is a value close to zero and the predicted function is indistinguishable from a constant function.

Effect of landscape forest cover on immigration rates

We captured 47 individuals of *M. incanus* 142 times in the three patches of the most forested landscape (50% forest cover), and 31 individuals 103 times in the three patches of the landscape with intermediate forest cover (30%). The best model among the demographic candidate models predicted both survival rates and population rate of change to be different between landscapes, but similar within each landscape, i.e. dependent on landscape context (Model I2, Table 1). Two models with fewer parameters were selected as equally plausible to the best model. The second selected model predicted constant survival rates and population rates of change between patches independent of landscape context (Model I1, Table 1), and the third model predicted survival rates to be dependent on landscape context, and population rates of change to be constant between patches independent of landscape context (Model I3, Table 1).

Weighted average estimates of population sizes are congruent with results from the first data set, resulting in higher values in patches of the most forested landscape (Table 2, Table S1). In this landscape, weighted averaged estimates of apparent survival as
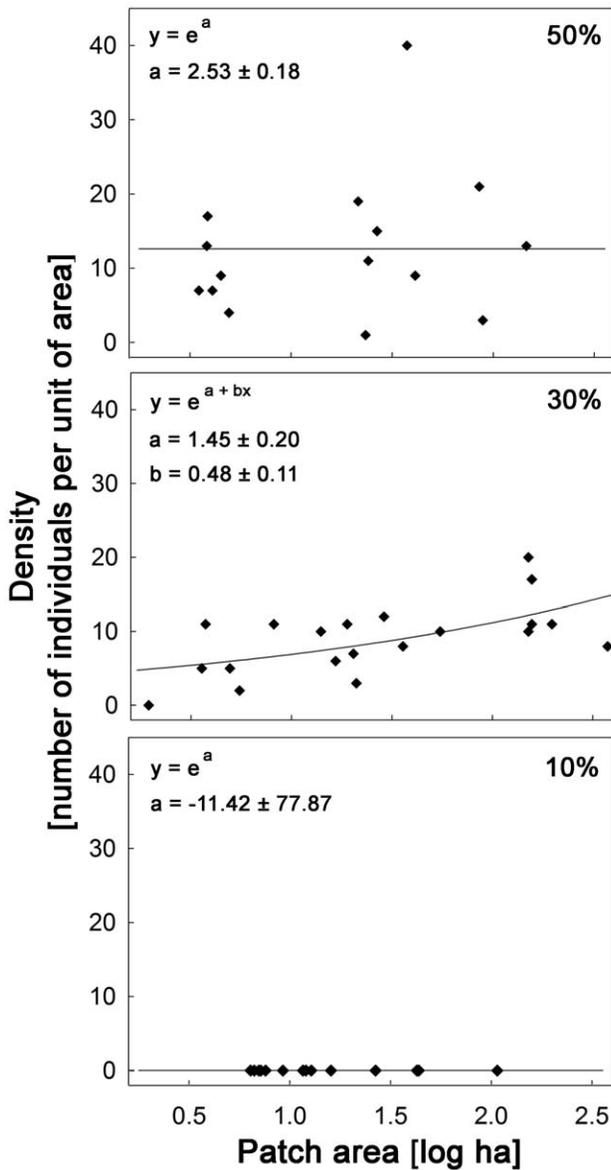
Figure 3. Observed (diamonds) and estimated (lines, Model D8) densities of *M. incanus*. Percentages (50%, 30%, 10%) represent the proportion of forest cover in three Atlantic forest landscapes in the Atlantic Plateau of São Paulo. Model equations and parameter estimates +/- SE are given in the upper left corners.
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Table 2. Model-averaged estimates of population sizes (N) of *M. incanus* in small patches of the landscape with 50% of remaining forest cover (patches 1 to 3) and of the landscape with 30% of remaining forest cover (patches 4 to 6), in primary capture sessions 1 to 5 between February and June 2008.

Amount of forest	Patch number	Primary capture session	N	Lower 95% CI	Upper 95% CI
50%	1	1	3.29	3.02	7.60
	1	2	4.47	2.41	16.73
	1	3	5.09	3.35	15.42
	1	4	5.13	5.01	7.69
	1	5	6.31	6.02	10.10
	2	1	3.08	3.00	5.21
	2	2	8.04	5.64	19.51
	2	3	5.25	4.19	12.33
	2	4	7.04	7.00	8.38
	2	5	8.10	8.00	10.31
	3	1	8.44	8.03	14.08
	3	2	13.23	8.70	29.79
	3	3	8.90	6.63	19.33
	3	4	8.10	8.00	10.26
	3	5	7.19	7.01	10.22
30%	4	1	2.01	2.00	2.55
	4	2	4.80	4.09	10.94
	4	3	3.26	3.02	6.71
	4	4	2.00	2.00	2.16
	4	5	1.00	1.00	1.20
	5	1	4.04	4.00	5.57
	5	2	1.37	1.03	5.71
	5	3	4.71	4.08	10.46
	5	4	4.01	4.00	4.55
	5	5	4.02	4.00	4.96
	6	1	5.00	5.00	5.05
	6	2	7.08	7.00	9.02
	6	3	6.02	6.00	6.89
	6	4	2.00	2.00	2.00
	6	5	1.00	1.00	1.01

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well as estimates of population rate of change were also slightly higher (Table 3). Further, numbers of immigrated individuals per capture session were significantly higher in patches of the most forested landscape (Fig. 4, $p = 0.043$).

Discussion

Landscape-level study designs (i.e. not only considering several patches in each landscape but also replicated landscapes) are challenging given the logistical difficulties of obtaining robust field data in a large number of sites. Our patch-level study, although limited by the small number of surveyed landscapes, provides evidence that population dynamics in patches depend on landscape context. Lower population sizes and lower number of immigrants of *M. incanus* into small patches in the landscape with 30% forest cover compared to patches in the most forested landscape are congruent with predictions from simulation models on the effects of landscape-wide habitat cover [10,14,15]. In combination with patch-area effects on *M. incanus* density being observed only in the landscape with 30% forest cover and the absence of the species in the most deforested landscape, these results are in accordance with the idea that variations in immigration rates represent the mechanism behind patch-area effects [9,20] and species extinction thresholds [13,18,19,43] across landscapes with differing proportions of remaining native vegetation. Thus, the results on the demography of a forest specialist species reported here are congruent with the patterns of diversity observed for the whole assemblage of forest specialist small mammals across the same landscapes [20].

Table 3. Model-averaged estimates of apparent survival rates and population rates of change of populations of *M. incanus* in small patches of the landscape with 50% of remaining forest cover (patches 1 to 3) and of the landscape with 30% of remaining forest cover (patches 4 to 6) between February and June 2008.

Parameter	Patch number	Estimate	Lower 95% CI	Upper 95% CI
Apparent survival rate 50% landscape	1	0.61	0.48	0.74
	2	0.62	0.48	0.74
	3	0.62	0.48	0.73
Apparent survival rate 30% landscape	4	0.50	0.35	0.66
	5	0.51	0.35	0.66
	6	0.50	0.34	0.66
Population rate of change 50% landscape	1	1.04	0.87	1.22
	2	1.04	0.87	1.21
	3	1.04	0.87	1.20
Population rate of change 30% landscape	4	0.93	0.37	1.00
	5	0.93	0.37	1.00
	6	0.93	0.38	1.00

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Although previous studies as far as we are aware did not investigate the effects of landscape context on immigration rates, immigration has consistently been shown to increase population size in patches both in field studies and simulation models [44–47]. Differences in population size among patches could also be caused by varying *in situ* recruitment rates, which we were not able to estimate due to low capture probabilities of young individuals. However, the observed number of young individuals in patches was similar among landscapes, suggesting that differences in population size were primarily driven by variation in immigration rates. In landscapes with a high proportion of remaining habitat and small distances among patches, high dispersal increases population size in patches, thereby rescuing small populations in small patches from the risk of local extinction [16,20]. As a consequence, population densities should be similar among patches irrespective of patch size, as we observed in this study. Given high dispersal between patches in the most forested landscape, the population of *M. incanus* can be classified as a patchy population (i.e. high dispersal rates between sub-populations effectively forming one population [48]). Indeed the confidence interval of the estimated population rate of change in small patches in this landscape encompasses the value of one, indicating that the higher immigration rate supports a constantly high population size.

On the other hand, not only was there a clear patch-area effect on the density of *M. incanus* in the landscape with intermediate forest cover (30%), but also the number of immigrants decreased significantly in small patches of this landscape in comparison to patches of the more forested landscape, despite the relatively small sample size and thus statistical power. Supposedly, the decrease in immigrants led to the comparatively lower population sizes in these patches. Further, the confidence intervals of the population rate of change only marginally encompass the value of one, indicating a slight decline in population size during the study. Although the time frame of the study is too short to infer general population trends, low population rate of change is considered a typical indicator of extinction risk [17,49], and this short-term population decline in these already small populations may indeed indicate an increased extinction risk from stochastic events. The lower immigration rates into small patches of this landscape with intermediate forest cover is presumed to be caused by increased inter-patch distances, which should increase the time spent in the matrix during dispersal events and thereby increase mortality and reduce dispersal success [50–53]. In the Atlantic forest, predation of forest marsupials by snakes and birds of prey has been shown to be higher in the open matrix than in forest patches [54,55]. The time an individual spends in the matrix might be additionally increased in landscapes with decreased native vegetation cover through reduced perception probability of neighboring suitable habitat patches [56,57]. Reduced or hindered neighborhood perception might result in non-optimal movements and hence longer times in the matrix and higher predation risk [58]. With a lower number of immigrants, but no complete isolation of local populations in patches, within-patch processes (births and deaths) should become relatively more important than between-patch processes, and the population can be described as a meta-population [59,60].

Increased isolation due to the reduction in the number of immigrants might also affect genetic diversity [61,62]. In an
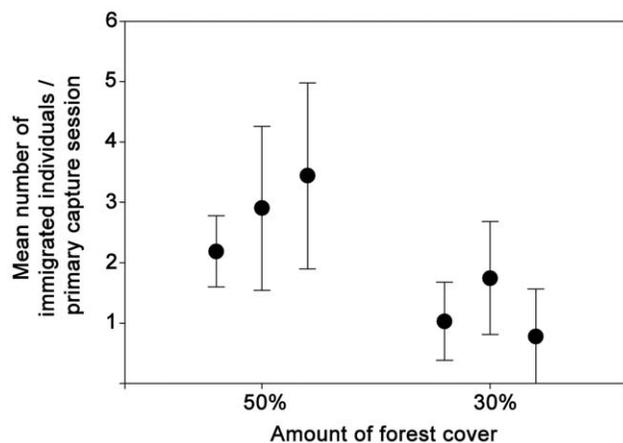

Figure 4. Mean number of immigrated individuals of *M. incanus* per capture session (+/- SE). Immigration into small patches was estimated at two Atlantic forest landscapes with different proportions of remaining forest (50% and 30%) in the Atlantic Plateau of São Paulo.
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investigation of genetic diversity in functional markers (Major Histocompatibility Complex, MHC) in the 30% forest cover landscape, Meyer-Lucht et al. [63,64] found surprisingly low numbers of alleles and associated higher parasite loads in populations of *M. incanus* compared to a sympatric didelphid marsupial, *Gracilinanus microtarsus*, which also occupies savanna-like habitats [65,66], and is considered less dependent on forest. Furthermore, a study on genetic variation based on non-functional markers (microsatellites) of populations of *M. incanus* in the same two landscapes found lower genetic diversity in populations of the less forested landscape (30%) as expected when dispersal between populations is reduced (Balkenhol, N., unpublished data).

Our results are also congruent with a fragmentation threshold sensu Andrén [9,12,20], namely a threshold in habitat amount below which patch-area effects become apparent, with a similar value to that proposed in a review of independent studies on birds and mammals (≤30% [9]). Furthermore, our results are in accordance with the notion that this threshold might be a first step leading to a drastic decrease in the probability of species persistence at the landscape scale (extinction threshold [18,19,43,67]), as recently proposed by Pardini et al. [20]. Given the similarity between *M. incanus* and several forest specialist small mammals in ecological requirements [25,26] and body size, the reduction in immigration rates, the variation in the strength of patch-area effects on population density, and the increased extinction probability across landscapes with decreasing proportion of forest cover are likely valid for other Atlantic forest species. The simultaneous extinction of forest specialist species in highly deforested landscapes would lead to an abrupt drop in gamma diversity [20,68].

Our study points out the value of single-species, process-oriented studies in understanding multi-species, larger-scale patterns [22]. While investigations of the effects of habitat fragmentation on population demography have focused almost exclusively on patches in single landscapes, our study provides empirical evidence for the dependence of population dynamics in patches on landscape context. By revealing immigration rates as a plausible candidate for the underlying mechanism causing both patch-area effects and species extinction thresholds, this study is in accordance with theoretical models proposing landscape-wide habitat cover as the main determinant of species persistence in fragmented landscapes [13,18,19]. This highlights the relevance of policies that promote landscape-wide preservation of native vegetation [68], such as the mandatory legislation to maintain native vegetation at a fixed percentage of private properties in Brazil (Forest Act [69,70]). Such policies are especially important in highly endangered biomes like the Atlantic forest, where more than 80% of all forest patches, representing more than 20% of the remaining forest area, are smaller than 50 ha [71].

Future research should investigate the influence of landscape-wide habitat amount on population demography in species varying in ecological traits, such as the degree of habitat specialization and dispersal ability, and in other ecosystems, as well as focus on the consequences of reduced immigration on genetic diversity, fitness and mating, and social systems.

Supporting Information

Figure S1 Detail of distribution of forest patches investigated for estimation of demographic parameters of *M. incanus*. (A) Fragmented landscape in Tapiraí - Piedade (50% forest cover) and (B) fragmented landscape in Ibiúna (30% forest cover). Forest patches are shown in gray. Dots: small forest patches where capture-recapture data was collected to estimate demographic parameters of populations of *M. incanus* (second dataset); circles: buffers around forest patches of a = 1 km, b = 1.5 km, and c = 2 km in which percentage of forest cover matches forest cover of the entire landscape.
(TIF)

Figure S2 Scheme of the 2-ha trapping grids used to capture *M. incanus*. Identical grids were installed at six forest patches located in two Atlantic forest landscapes with different proportions of remaining forest (50% and 30%) in the Atlantic Plateau of São Paulo (second dataset). White rectangles: Sherman traps; black circles: pitfall traps; black lines: plastic fence connecting pitfall traps of one line.
(TIF)

Table S1 Model-averaged estimates of population sizes of adults ($N_{(adult)}$) of *M. incanus* in small patches of the landscape with 50% of remaining forest cover (patches 1 to 3) and of the landscape with 30% of remaining forest cover (patches 4 to 6), in primary capture sessions 2 to 5 between February and June 2008.
(DOC)

Acknowledgments

Author Contributions

Conceived and designed the experiments: TP RP. Performed the experiments: TP AAB CdSdB RP. Analyzed the data: TP AAB CdSdB RP. Contributed reagents/materials/analysis tools: SS RP. Wrote the paper: TP AAB CdSdB SS RP.

References

1. Chiarello AG (2000) Density and population size of mammals in remnants of Brazilian Atlantic forest. Conserv Biol 14: 1649–1657.
2. Stoll P, Oggier P, Baur B (2009) Population dynamics of six land snail species in experimentally fragmented grassland. J Anim Ecol 78: 236–246.
3. Johannesen E, Andreassen HP, Ims RA (2000) Spatial explicit demography: The effects habitat patch isolation have on vole matrilines. Ecol Lett 3: 48–57.
4. Coffman CJ, Nichols JD, Pollock KH (2001) Population dynamics of *Microtus pennsylvanicus* in corridor-linked patches. Oikos 93: 3–21.
5. Ruiz-Gutierrez V, Gavin TA, Dhondt AA (2008) Habitat fragmentation lowers survival of a tropical forest bird. Ecol Appl 18: 838–846.
6. Gardner JL, Heinsohn RG (2007) Probable consequences of high female mortality for speckled warblers living in habitat remnants. Biol Conserv 135: 473–483.
7. Cushman SA (2006) Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biol Conserv 128: 231–240.
8. Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. Global Ecol Biogeogr 16: 265–280.
9. Andrén H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71: 355–366.
10. With KA, King AW (1999) Dispersal success in fractal landscapes: a consequence of lacunarity thresholds. Landscape Ecol 14: 78–83.
11. Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34: 487–515.
12. Swift TL, Hannon SJ (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. Biol Rev 85: 35–53.
13. With KA, King AW (1999) Extinction thresholds for species in fractal landscapes. Conserv Biol 13: 314–326.
14. Bender DJ, Tischendorf L, Fahrig L (2003) Using patch isolation metrics to predict animal movement in binary landscapes. Landscape Ecol 18: 17–39.

15. Tischendorf L, Bender DJ, Fahrig L (2003) Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. Landscape Ecol 18: 41–50.

16. Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58: 445–449.

17. Gaggiotti OE, Hanski I (2004) Mechanisms of population extinction. In: Hanski I, Gaggiotti OE, eds. Metapopulation dynamics: perspectives from landscape ecology. Burlington San Diego, London: Elsevier Academic Press. pp 337–366.

18. Fahrig L (2001) How much habitat is enough? Biol Conserv 100: 65–74.

19. Fahrig L (2002) Effect of habitat fragmentation on the extinction threshold: a synthesis. Ecol Appl 12: 346–353.

20. Pardini R, Bueno AA, Gardner TA, Prado PI, Metzger JP (2010) Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. Plos One 5: e13666. doi:10.1371/journal.pone.0013666.

21. Bennett AF, Radford JQ, Haslem A (2006) Properties of land mosaics: Implications for nature conservation in agricultural environments. Biol Conserv 133: 250–264.

22. Lindenmayer DB, Fischer J, Felton A, Montague-Drake R, Manning A, et al. (2007) The complementarity of single-species and ecosystem-oriented research in conservation research. Oikos 116: 1220–1226.

23. Fernandes FR, Cruz LD, Martins EG, dos Reis SF (2010) Growth and home range size of the gracile mouse opossum Gracilinanus microtarsus (Marsupialia: Didelphidae) in Brazilian cerrado. Growth and home range size of the gracile mouse opossum Gracilinanus microtarsus (Marsupialia: Didelphidae) in Brazilian cerrado 26: 185–192.

24. Gentile R, Finotti R, Rademaker V, Cerqueira R (2004) Population dynamics of four marsupials and its relation to resource production in the Atlantic forest in southeastern Brazil. Mammalia 68: 109–119.

25. Umetsu F, 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.

26. Püttker T, Pardini R, Meyer-Lucht Y, Sommer S (2008) Responses of five small mammal species to micro-scale variations in vegetation structure in secondary Atlantic Forest remnants, Brazil. BMC Ecol 8: doi:10.1186/1472-6785-1188-1189.

27. Oliveira-Filho AT, Fontes MAL (2000) Patterns of floristic differentiation among Atlantic Forests in Southeastern Brazil and the influence of climate. Biotropica 32: 793–810.

28. Ross JLS, Moroz IC (1997) Mapa Geomorfológico do Estado de São Paulo: escala 1:500.000. FFLCH-USP. São Paulo: IPT and Fapesp.

29. Agritempo Sistema de Monitoramento Agrometorológico. Agritempo Website. Available: http://www.agritempo.gov.br. Accessed 2011 Sep.

30. Umetsu F, Naxara L, Pardini R (2006) Evaluating the efficiency of Pitfall traps for sampling small mammals in the Neotropics. J Mammal 87: 757–765.

31. Pollock KH (1982) A capture-recapture design robust to unequal probability of capture. J Wildl Manage 46: 752–757.

32. Kendall WL, Nichols JD, Hines JE (1997) Estimating temporary emigration using capture-recapture data with Pollocks robust design. Ecology 78: 563–578.

33. Kendall WL, Pollock KH (1992) The Robust Design in capture-recapture studies: a review and evaluation by Monte Carlo simulation. In: McCullough DR, Barrett RH, eds. Wildlife 2001: Populations. London: Elsevier. pp 31–43.

34. Burnham KP, Anderson DR (2002) Model selection and multimodel inference - a practical information-theoretic approach. New York, USA: Springer Science + Business Media. 484 p.

35. R Development Core Team (2010) R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. Available: http://www.R-project.org. Accessed 2011 Sep.

36. White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46: 120–139.

37. Stanley TR, Burnham KP (1999) A closure test for time-specific capture-recapture data. Environ Ecol Stat 6: 197–209.

38. Pradel R (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth rate. Biometrics 52: 703–709.

39. Huggins RM (1991) Some practical aspects of a conditional likelihood approach to capture experiments. Biometrics 47: 725–732.

40. Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19: 101–108.

41. Beck H, Gaines MS, Hines JE, Nichols JD (2004) Comparative dynamics of small mammal population in treefall gaps and surrounding understorey within Amazonian rainforest. Oikos 106: 27–38.

42. Macedo J, Loretto D, Vieira MV, Cerqueira R (2006) Classes de desenvolvimento em marsupiais: um método para animais vivos. Mastozool Neotrop 13: 133–137.

43. Lande R (1987) Extinction thresholds in demographic models of territorial populations. Am Nat 130: 624–635.

44. Fahrig L, Paloheimo J (1988) Determinants of local population size in patchy habitats. Theor Popul Biol 34: 194–213.

45. Paradis E (1995) Survival, immigration and habitat quality in the Mediterranean pine vole. J Anim Ecol 64: 579–591.

46. Debinski DM, Holt RD (2000) A survey and overview of habitat fragmentation experiments. Conserv Biol 14: 342–355.

47. Bowman J, Cappuccino N, Fahrig L (2002) Patch size and population density: the effect of immigration behavior. Conserv Ecol 6: http://www.consecol.org/vol6/iss1/art9.

48. Harrison S (1991) Local extinction in a metapopulation context: an empirical evaluation. Biol J Linn Soc 42: 73–88.

49. Sibly RM, Hone J (2002) Population growth rate and its determinants: an overview. Philos T Roy Soc B 357: 1153–1170.

50. Andreassen HP, Ims RA (1998) The effects of experimental habitat destruction and patch isolation on space use and fitness parameters in female root vole Microtus oeconomus. J Anim Ecol 67: 941–952.

51. Aars J, Johannesen E, Ims RA (1999) Demographic consequences of movements in subdivided root vole populations. Oikos 85: 204–216.

52. Smith JE, Batzli GO (2006) Dispersal and mortality of prairie voles (Microtus ochrogaster) in fragmented landscapes: a field experiment. Oikos 112: 209–217.

53. Gruber B, Henle K (2008) Analysing the effect of movement on local survival: a new method with an application to a spatially structured population of the arboreal gecko Gehyra variegata. Oecologia 154: 679–690.

54. Lira PK, Fernandez FAD, Carlos HSA, Curzio PD (2007) Use of a fragmented landscape by three species of opossum in south-eastern Brazil. J Trop Ecol 23: 427–435.

55. Bernardo LRR (2010) Comportamento de procura de habitats de Philander frenatus (Olfers, 1818) em remanescentes de Mata Atlântica do Rio de Janeiro. MSc Dissertation, Federal University of Rio de Janeiro, Rio de. pp Janeiro.76.

56. Zollner PA, Lima SL (1999) Search strategies for landscape-level interpatch movements. Ecology 80: 1019–1030.

57. Forero-Medina G, Vieira MV (2009) Perception of a fragmented landscape by neotropical marsupials: effects of body mass and environmental variables. J Trop Ecol 25: 53–62.

58. Fahrig L (2007) Non-optimal animal movement in human-altered landscapes. Funct Ecol 21: 1003–1015.

59. Thomas CD, Kunin WE (1999) The spatial structure of populations. J Anim Ecol 68: 647–657.

60. Hanski I, Gaggiotti OE (2004) Ecology, Genetics, and Evolution of Metapopulations. BurlingtonSan Diego, , London: Elsevier Academic Press. pp 696.

61. Frankham R, Ballou JD, Briscoe DA (2002) Introduction to Conservation Genetics. Cambridge: Cambridge University Press. pp 617.

62. Banks SC, Lindenmayer DB, Ward SJ, Taylor AC (2005) The effects of habitat fragmentation via forestry plantation establishment on spatial genotypic structure in the small marsupial carnivore, Antechinus agilis. Mol Ecol 14: 1667–1680.

63. Meyer-Lucht Y, Otten C, Püttker T, Sommer S (2008) Selection, diversity and evolutionary patterns of the MHC class II DAB in free-ranging Neotropical marsupials. BMC Genet 9: doi:10.1186/1471-2156-1189-1139.

64. Meyer-Lucht Y, Otten C, Püttker T, Pardini R, Metzger JP, et al. (2010) Variety matters: adaptive genetic diversity and parasite load in two mouse opossums from the Brazilian Atlantic forest. Conserv Genet 11: 2001–2013.

65. Martins EG, Bonato V, Pinheiro A, Dos Reis SF (2006) Variation in the food-niche width of Gracilinanus microtarsus (Didelphimorphia: Didelphidae) in a cerrado remnant in south-eastern Brazil. Mamm Biol 71: 304–308.

66. Martins EG, Bonato V, Queiroz da-Silva C, Reis F (2006) Seasonality in reproduction, age structure and density of the gracile mouse opossum Gracilinanus microtarsus (Marsupialia: Didelphidae) in a Brazilian cerrado. J Trop Ecol 22: 461–468.

67. Andrén H (1996) Population responses to habitat fragmentation: Statistical power and the random sample hypothesis. Oikos 76: 235–242.

68. Hanski I (2011) Habitat loss, the dynamics of biodiversity, and a perspective on conservation. AMBIO 40: 248–255.

69. Metzger JP (2010) O código florestal tem base científica? Conservação & Natureza 8: 92–99.

70. Metzger JP, Lewinsohn TM, Joly CA, Verdade LM, Martinelli A, et al. (2010) Brazilian law: full speed in reverse? Science 329: 276–277.

71. Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM (2009) The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biol Conserv 142: 1141–1153.