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**Landscape Ecology**

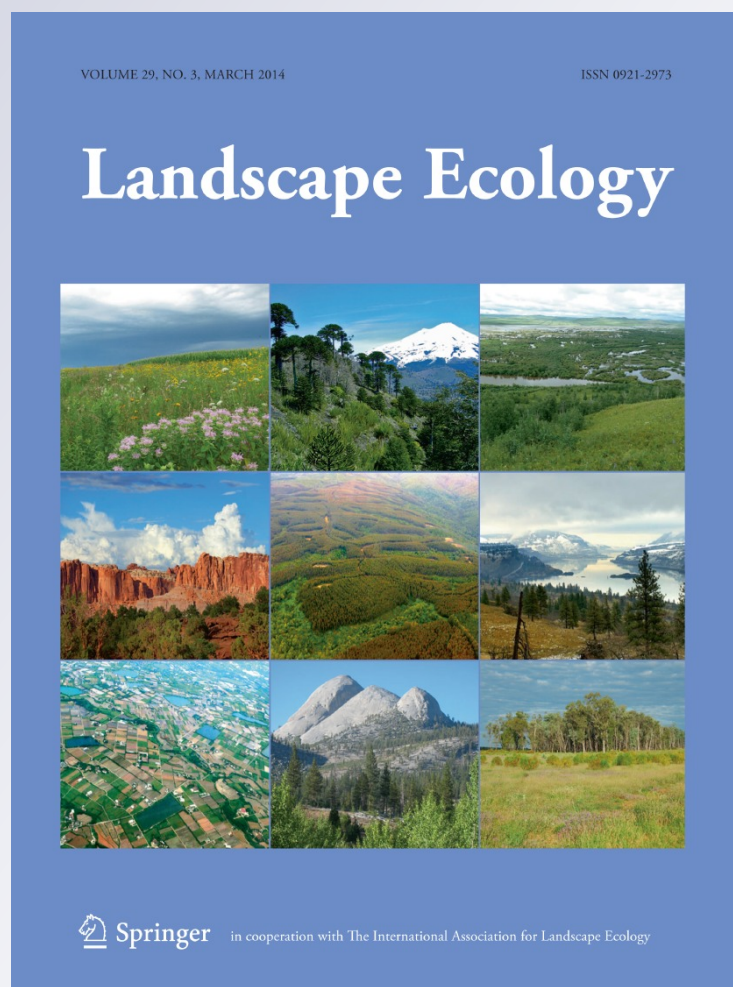
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# The effects of the number, size and isolation of patches along a gradient of native vegetation cover: how can we increment habitat availability?

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**Abstract** Habitat availability—or how much habitat species can reach at the landscape scale—depends primarily on the percentage of native cover. However, attributes of landscape configuration such as the number, size and isolation of habitat patches may have complementary effects on habitat availability, with implications for the management of landscapes. Here, we determined whether, and at which percentages of native cover, the number, size and isolation of patches contribute for habitat availability. We quantified habitat availability in 325 landscapes spread across the state of Rio de Janeiro, in the Atlantic Forest hotspot, with either high (>50 %), intermediate (50–30 %), low (30–10 %) or very low (<10 %) percentage of native cover, and for six hypothetical species differing in inter-patch dispersal ability.

Above 50 % of native cover, the percentage of cover per se was the only determinant of habitat availability, but below 50 % the attributes of landscape configuration also contributed for habitat availability. The number of patches had a negative effect on habitat availability in landscapes with 50–10 % of native cover, whereas patch size had a positive effect in landscapes with <10 % of native cover. The different species generally responded to the same set of landscape attributes, although to different extents, potentially facilitating decision making for conservation. In landscapes with >50 % of native cover, conservation actions are probably sufficient to guarantee habitat availability, whereas in the remaining landscapes additional restoration efforts are needed, especially to reconnect and/or enlarge remaining habitat patches.

**Keywords** Brazilian Atlantic Forest · Connectivity conservation · GIS · Habitat fragmentation · Landscape metrics · Restoration

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## Introduction

The process of habitat loss and fragmentation causes profound alterations in the amount and configuration of habitat in landscapes (Ewers and Didham 2006; Fisher and Lindenmayer 2007). The reduction in the total amount of native vegetation cover is generally considered the most deleterious consequence of this process on biodiversity (Andrén 1994; Fahrig 2003;

Ewers and Didham 2006; Fischer and Lindenmayer 2007; Pardini et al. 2010). Such reduction leads to further changes in landscape configuration, including a decrease in mean patch size, an increase in patch isolation, and changes in the number of patches, which tends to be higher at intermediate percentages of native vegetation cover (Andrén 1994; Fahrig 2003). The changes in such attributes of landscape configuration are usually non-linearly related to reductions in the amount of native vegetation cover (Fahrig 2003; Ewers and Didham 2006), potentially leading to sudden alterations on dispersal success (With and King 1999), immigration rates (Püttker et al. 2011) and landscape connectivity (Metzger and Décamps 1997), ultimately affecting species abundance and richness (Pardini et al. 2010). A central challenge is to determine whether, and at which percentages of native cover, the number, size and isolation of patches influence biodiversity, information needed to propose effective conservation and restoration actions for landscapes (Fahrig 2003; Lindenmayer et al. 2008; Martensen et al. 2012; Villard and Metzger in press).

Two theoretical models considering processes at both landscape and local scales were proposed to explain the effects of reducing native vegetation cover on population persistence. The Fragmentation Threshold model (Andrén 1994) suggests the existence of a threshold in the amount of native vegetation cover at the landscape scale. Below a certain amount of native vegetation cover, for example 30–10 % depending on the species' dispersal ability, population persistence becomes dependent on the size and isolation of patches. The threshold results from a reduction in patch size and an exponential increase in patch isolation, which hampers movement of species between patches (Andrén 1994). On the other hand, the Regime Shift model (Pardini et al. 2010) predicts that the effects of the size and isolation of patches are evident only at “intermediate” amounts of native vegetation cover (e.g. ~30 %), when immigration rates tend to be insufficient to maintain populations in small patches. At higher percentages of native vegetation cover (e.g. ~50 %), immigration rates are high enough to maintain populations even in small patches, while at lower percentages of cover (e.g. ~10 %) immigration rates are eroded due to the exponential increase in patch isolation, and even populations in large patches become subject to local extinction. As a consequence, the process of habitat loss and

fragmentation could lead to a regime shift, characterized by the irreversible loss of habitat specialist species, and a reduction in richness at both landscape and local scales (Pardini et al. 2010).

To avoid the loss of habitat specialist species at the landscape scale, it is essential to maximize the amount of habitat available for these species, because the number of individuals of any species supported in a landscape is closely linked to the amount of habitat (Hubbell 2001; Fahrig 2003). In this sense, the concept of habitat availability, or how much habitat species can reach in the landscape, becomes particularly useful (Pascual-Hortal and Saura 2006). Habitat availability depends on a patch attribute (e.g. patch size) and also on functional connectivity, because large but isolated patches will not be reached by—and thus will be unavailable for—individuals inhabiting other patches (Pascual-Hortal and Saura 2006; Luque et al. 2012). Habitat availability may vary according to species' dispersal abilities (Saura and Rubio 2010) and may affect the occurrence of species across different patches in a landscape (Awade et al. 2012; Decout et al. 2012). By comparing habitat availability among different landscapes, it would be possible to determine the relative contribution of different attributes of landscape configuration for habitat availability. Quantifying habitat availability and understanding how it is affected by different attributes of landscape configuration may offer valuable insights for decision making in conservation and restoration planning (Saura and Pascual-Hortal 2007; Awade et al. 2012; Luque et al. 2012; Crouzeilles et al. 2013).

In this paper we determined the relative contribution of the number, size and isolation of patches for habitat availability in landscapes encompassing a gradient of native vegetation cover. Our main hypothesis was that the relative contribution of the number, size and isolation of patches for habitat availability depends on the percentage of native cover at the landscape scale. In testing this hypothesis, we compared predictions of the Fragmentation Threshold and Regime Shift models. The former predicts stronger effects of patch size and isolation at landscapes with  $\leq 30\%$  of native cover, while the later predicts stronger effects of patch size and isolation only at landscapes with “intermediate” cover (~30 %). We also contrasted responses of six hypothetical species differing in inter-patch dispersal abilities (10, 50, 200, 500, 1000 or 3000 m). Analyses encompassed 325

landscapes of the Atlantic Forest hotspot, spread across the entire state of Rio de Janeiro in Brazil, and categorized in four scenarios of native cover: high (>50 %), intermediate (50–30 %), low (30–10 %) or very low (<10 %). The Atlantic Forest is an invaluable laboratory to understand the effects of habitat fragmentation in tropical regions, due to the high heterogeneity of land use (Laurance 2009) and the varying levels of habitat loss and fragmentation (Ribeiro et al. 2009).

## Methods

### Study area

Rio de Janeiro is located at the southeastern coast of the Brazilian Atlantic Forest, with an area of ca. 43,700 km<sup>2</sup>. Currently, the state is inhabited by approximately 16 million people (<http://ibge.gov.br/estadosat/perfil.php> accessed on April 2012) and less than 20 % of its native forest cover still remains (SOS Mata Atlântica and INPE 2010). The process of habitat loss and fragmentation in this region was driven mainly by socio-economic pressures, resulting in different types of land use such as agriculture, pastures and urban areas, which surround more than 10,000 forest fragments. Approximately 85 % of these fragments have less than 100 ha, totaling 20 % of the remaining forest cover in Rio de Janeiro, while only 70 fragments have more than 1000 ha and represent 67 % of the remaining cover (Fidalgo et al. 2009). Remnant forest data were obtained from the map produced by SOS Mata Atlântica and INPE (2010), derived from TM/Landsat 5, ETM+/Landsat 7 or CCD/CBERS-2 images (Ponzoni et al. 2012), available at a scale of 1:50,000 in vector format, and delimiting remnants  $\geq 3$  ha (Fig. 1). All geographic information system data were converted to UTM projection to assure accurate area and distance calculations.

We divided Rio de Janeiro in hexagons of 10,000 ha, each hexagon representing a different landscape used as the unit of analysis. The size of the hexagons was determined following three criteria: (i) hexagons were large enough to allow the inclusion of species with large dispersal abilities (3000 m) in the analysis, (ii) the total number of landscapes within each scenario of native vegetation cover was large enough for robust analyses, and (iii) other studies in the Atlantic Forest have used

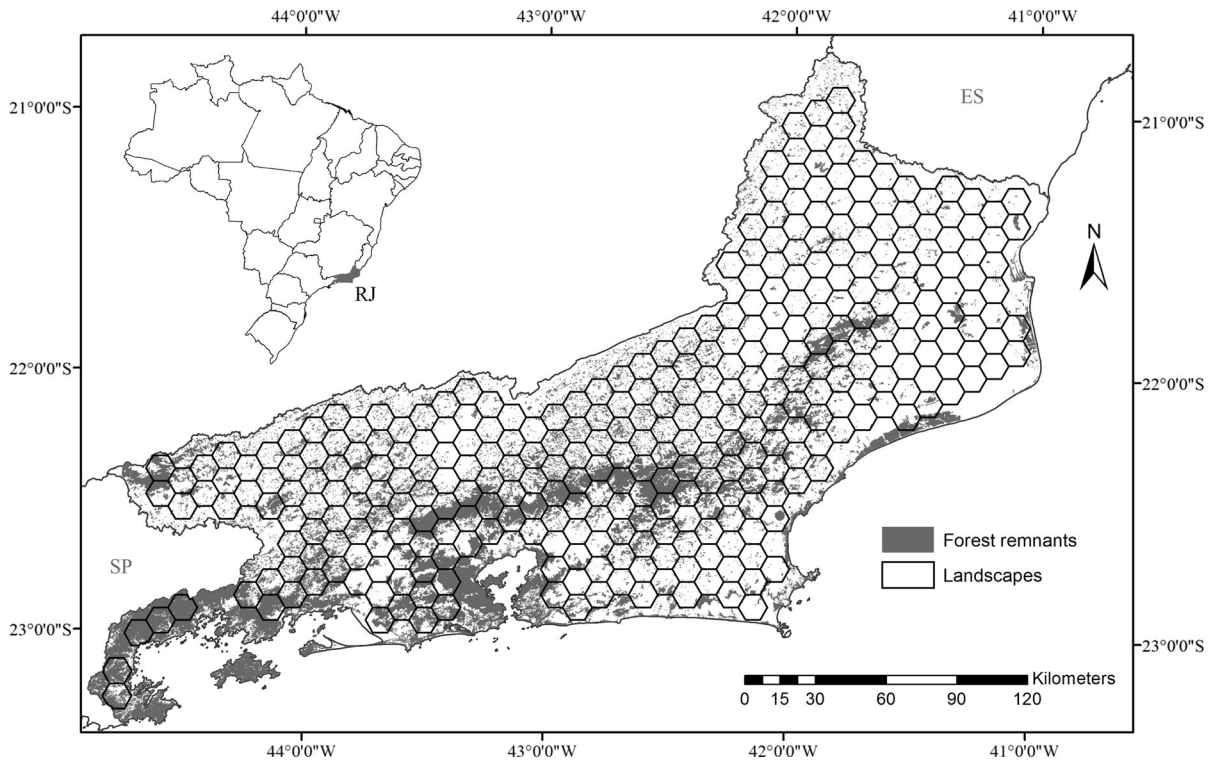
10,000 ha landscapes to study the effects of habitat loss and fragmentation (e.g. Pardini et al. 2010; Püttker et al. 2011), facilitating comparisons. We considered only landscapes entirely contained within the boundaries of Rio de Janeiro, totalizing 325 landscapes (Fig. 1).

### Quantifying habitat availability

We quantified habitat availability at the landscape scale using the Probability of Connectivity index (*PC*; Saura and Pascual-Hortal 2007). This index considers that the amount of habitat actually available to individuals depends on a patch attribute and also on functional connectivity, and can be partitioned into three fractions (Saura and Rubio 2010). The patch attribute may be determined by its size, habitat quality or other characteristics (named “intra” fraction), while connectivity is determined by flux weighted by area (“flux” fraction) and the topological position of a patch in the network (“connector” fraction), according to the probability of dispersal of the species (Saura and Rubio 2010). *PC* calculates the probability of dispersal between two patches as a decreasing function of inter-patch Euclidean or effective distance (Saura and Pascual-Hortal 2007), as:

$$PC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i \cdot a_j \cdot P_{ij}^*}{A_L^2} \quad (1)$$

where  $n$  is the number of patches,  $a_i$  and  $a_j$  are the attributes of the respective patches (e.g. patch size),  $P_{ij}^*$  is the maximum product probability of all possible paths between patches  $i$  and  $j$ , and  $A_L^2$  is the square of the geographic area of the landscape (Saura and Pascual-Hortal 2007). The probability of connection between two patches depends on the dispersal ability of the species and the presence of intermediate stepping-stone patches facilitating movement. The probability of a path—defined as a possible trajectory from one patch to another—is the product of dispersal probabilities for all connections in the way. Thus, the maximum product probability is the path with highest connection probability among all possibilities between two specified patches. *PC* values vary from 0 (no habitat available) to 1 (all the landscape is occupied by habitat). We used patch size as the patch attribute, Euclidean distance between patches as the connection attribute, and dispersal values corresponding to a probability of 50 % of direct dispersal between



**Fig. 1** Distribution of Atlantic Forest remnants (in gray) across the state of Rio de Janeiro, southeastern Brazil. The 325 hexagons represent only landscapes entirely located within the

boundaries of Rio de Janeiro. These different landscapes were used as units of analysis

patches, to generate the negative exponential function of inter-patch Euclidean distance. We used Euclidian rather than effective distances because our focus was on the effects of the number, size and isolation of patches, which could be obscured by including matrix effects (Bender and Fahrig 2005).

To evaluate how habitat availability at a given landscape varies according to the dispersal abilities of the focal species, we contrasted species with short (10 or 50 m), medium (200 or 500 m) or large (1000 or 3000 m) abilities to perform inter-patch movements, based on empirical data for Atlantic Forest species compiled by Crouzeilles et al. (2010). These dispersal values correspond to 50 % of probability of direct dispersal between two patches, representing median dispersal distances. Because our aim was to evaluate the effect of dispersal ability only, we kept other functional traits similar among species, such as habitat specificity and minimum patch size required. Therefore, all species compared were forest specialists that might occur in remnants  $\geq 3$  ha. Analyses of habitat

availability were performed using the software Conefor Sensinode 2.5.8 command line version ([www.conefor.org](http://www.conefor.org); Saura and Torné 2009).

#### Explanatory variables

The total amount of native vegetation cover (NC) was quantified as the percentage of remnant forest within each landscape. This metric represents the effect of habitat loss independently of its subdivision. We also quantified three widely used metrics of landscape configuration (Fahrig 2003): number of patches (NP), mean patch size (PS), and mean patch isolation (PI). Patch isolation was determined as the mean distance among all patches. Habitat availability tends to be higher in landscapes with few, larger and/or less isolated patches for the same amount of native cover (Saura and Pascual-Hortal 2007). All variables were measured using the software ArcGis 9.3 (ESRI 2008).

To test our main hypothesis, and also to compare the predictions of the Fragmentation Threshold and Regime Shift models, we categorized the 325 landscapes into four scenarios of native cover for analysis: high (>50 %;  $n = 26$  landscapes), intermediate (50–30 %;  $n = 38$ ), low (30–10 %;  $n = 107$ ) and very low native cover (<10 %;  $n = 154$ ). We excluded five landscapes because they had substantially fewer patches or higher patch sizes than other landscapes in the same scenario. To assist in the interpretation of results, we correlated all explanatory variables (NC, PI, NP, and PS) separately for each scenario of native cover. Except for landscapes with very low cover (<10 %), PS and NP, as well as PI and PS, were negatively related (Spearman's  $r \leq -0.78$  and  $\leq -0.52$ , respectively), whereas PI and NP were positively related ( $r \geq 0.56$ ). The NC had a positive relationship with PS in all scenarios (Spearman's  $r \leq 0.46$ ), a positive relationship with NP in landscapes with very low cover ( $r = 0.76$ ), and a negative relationship in landscapes with intermediate cover ( $r = -0.52$ ).

#### Data analysis

We used an information theoretic approach (Burnham and Anderson 2002) to compare the relative contribution of NC, PI, NP and PS for habitat availability. We performed 24 separate analyses, one analysis for each combination of species' dispersal ability (10, 50, 200, 500, 1000 or 3000 m) and scenario of native cover (>50, 50–30, 30–10 or <10 %). Because habitat availability was strongly related to NC (see Fig. 2), we included NC in all models as a covariate. Thus, in each analysis, we contrasted four competing generalized linear models, one reference model containing only native vegetation cover (NC), and three other models containing NC plus either PI, NP or PS. This approach allowed evaluating whether, and at which percentages of native cover, such attributes of landscape configuration affect habitat availability in addition to NC. Habitat availability was modeled assuming a beta distribution, because the values were continuous but bounded between 0 and 1 (Bolker 2008). We used a probit link function for all models. We calculated for each candidate model the Akaike Information Criterion corrected for small samples (AICc), the  $\Delta_i$  ( $=\text{AICc}_i - \text{minimum AICc}$ ) and the Akaike weight ( $w_i$ ), which indicates the probability

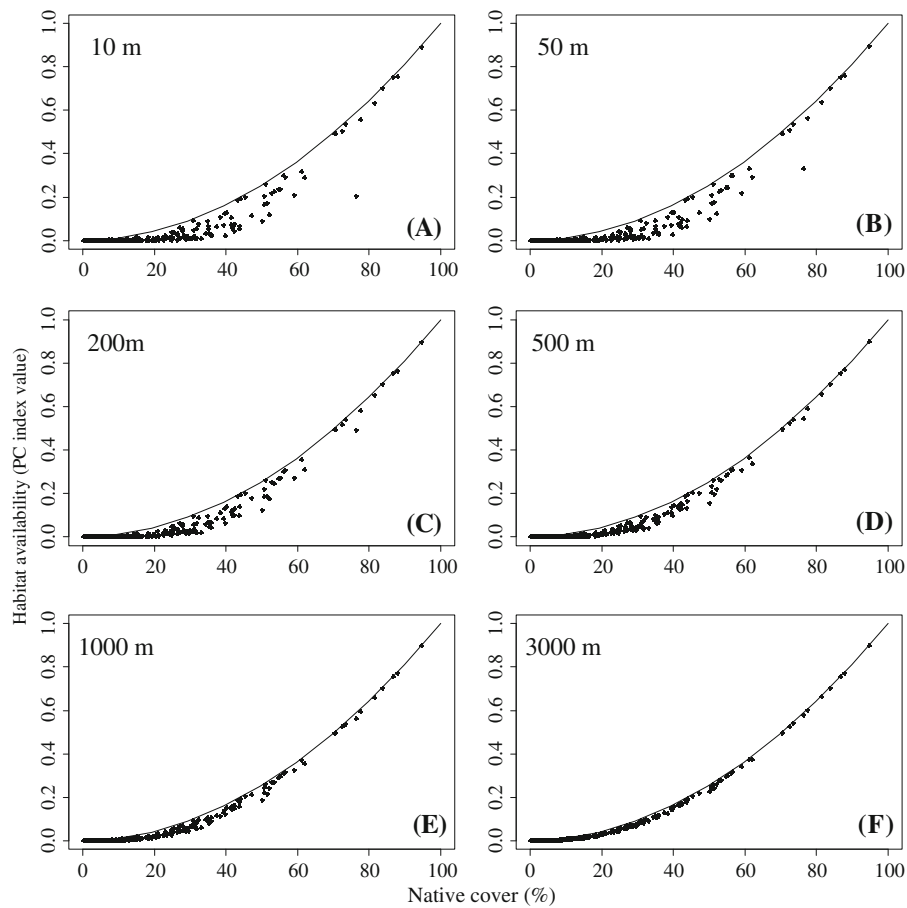
that the model  $i$  is the best model within the set (Burnham and Anderson 2002). Models with  $0 < \Delta_i \leq 2$  were considered equally plausible to the top-ranked model ( $\Delta_i = 0$ ), unless they differed from that model by containing only one extra (additional) parameter, which was then considered uninformative (Burnham and Anderson 2002; Arnold 2010). All analyses were carried out in the R 2.12 environment (R Development Core Team 2010), using the package “betareg” (Zeileis et al. 2012).

#### Results

Habitat availability had a clearly non-linear, exponential relationship with the total amount of native cover for the six species analyzed (Fig. 2). The relationship was particularly clear for the more mobile species (3000 m), whereas the scatter of points increased as species' dispersal abilities decreased, reflecting deviations from the maximum possible values of habitat availability at a given amount of native cover (Fig. 2). In general, both the median and the variability in habitat availability values increased with increasing dispersal abilities (Fig. 3). Variability within and among species was higher in landscapes with low (30–10 %) native cover, and lower in landscapes with intermediate (50–30 %) or high (>50 %) native cover (Fig. 3).

The relative contributions of patch isolation (PI), number of patches (NP) and patch size (PS) for habitat availability varied among the four scenarios of native cover, with patterns often (but not always) consistent among different species (Table 1). In landscapes with high native cover (>50 %), the reference model, containing NC only, was always ranked as the most plausible one (Table 1). For some species, PI, NP and/or PS were also present in addition to NC in models with  $\Delta_i \leq 2$ , but in all cases their inclusion did not improve substantially model fit compared to the model with NC only, hence these parameters did not affect substantially habitat availability (Table 1).

In landscapes with intermediate native cover (50–30 %), the NP, in addition to NC, was the main factor affecting habitat availability for all species ( $w_i$  for NP varying from 0.67 to 0.94, Table 1). In addition, for the more mobile species (3000 m), the model NC + PI was also plausible, because it had a  $\Delta_i < 2$  and differed from the top-ranked model



**Fig. 2** Relationship between percentage of native cover and habitat availability across 325 Atlantic Forest landscapes, for six species with different inter-patch dispersal abilities (10, 50, 200, 500, 1000 and 3000 m). Habitat availability values were calculated for each species at each landscape using the

(NC + NP) by containing an alternative (and not merely an additional) parameter. Thus, PI also contributed to habitat availability, although to a lower extent ( $w_i = 0.25$ ) than NP. Both NP and PI were negatively related to habitat availability.

In landscapes with low native cover (30–10 %), habitat availability depended on the NP, in addition to NC, for all species ( $w_i$  for NP = 1.00 for species with dispersal ability  $\leq 1000$  m, and  $w_i = 0.34$  for species with dispersal ability = 3000 m). For species with dispersal abilities  $\leq 1000$  m, the model with NC + NP was the only one considered plausible. For the more mobile species (3000 m), the model NC + NP was again plausible but ranked only as the second best one, with NC + PS being the most plausible model, indicating that PS was the main factor affecting habitat

Probability of Connectivity index (PC). Black lines are the maximum value of the PC index for each percentage of native cover, which occurs when all habitat is concentrated in a single patch

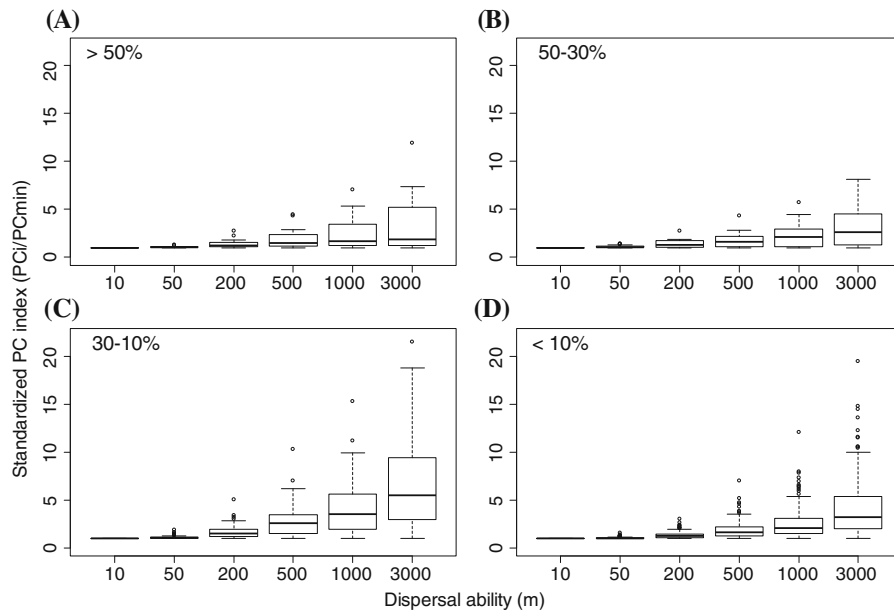
availability ( $w_i = 0.66$ ; Table 1). Habitat availability was negatively related to NP and positively related to PS.

Finally, in landscapes with very low native cover ( $< 10$  %), habitat availability depended strongly on PS, in addition to NC, for all species ( $w_i$  for NP = 1.00 for all species). The model NC + PS was always the only plausible one, and habitat availability was always positively related to PS.

## Discussion

For all species, habitat availability depended primarily on the amount of native cover at the landscape scale, in accordance with the view that habitat loss is the main





**Fig. 3** Variation of habitat availability with inter-patch dispersal ability of species (10, 50, 200, 500, 1000 and 3000 m) across 325 Atlantic Forest landscapes. Analyses were carried out separately for landscapes with very high (>50 %), high (50–30 %) intermediate (30–10 %) or low (<10 %) percentage of native cover. Symbols include the median (horizontal line),  $\pm 1$  SE (box), the 95 % confidence interval (vertical lines) and outliers (points). Habitat availability values were calculated for

cause of biodiversity decline in fragmented landscapes (Fahrig 2003). The relationship between native cover and habitat availability, as quantified through the Probability of Connectivity index ( $PC$ ), was clearly non-linear but exponential. This pattern reflects the fact that the numerator in the index multiplies the patch attributes (areas; Saura and Pascual-Hortal 2007), thus habitat availability tends to increase exponentially as native cover increases. The maximum value of the  $PC$  index for each percentage of native cover occurs when all habitat is concentrated in a single patch (black lines in Fig. 2). Departures from the maximum values are possible, reflecting the influence of attributes of landscape configuration, and species dispersal abilities. Such departures were especially evident for the less mobile species (Fig. 2), whose limited dispersal ability reduces the probability of connection between patches, suggesting that these species are more strongly affected by landscape configuration compared to more mobile species. These results are in accordance with many empirical studies showing that species with short gap-crossing ability

each species at each landscape using the Probability of Connectivity index ( $PC$ ). The graphs depict standardized values, calculated within each landscape by dividing the  $PC$  value of each species by the smaller value obtained in that landscape. Standardized values thus indicate how larger was the  $PC$  value of a species in a given landscape compared to the smallest  $PC$  value obtained in the same landscape

are more sensitive to habitat loss and fragmentation (review in Henle et al. 2004; Awade et al. 2012; Martensen et al. 2012). The higher variability in habitat availability among and within species occurred in landscapes with 30–10 % of cover, probably because variation in the attributes of landscape configuration was maximal at these percentages, what may be the pattern for most landscapes (Villard and Metzger in press).

We confirmed the hypothesis that the effects of the number, size and isolation of patches varies with the total amount of habitat at the landscape scale. In landscapes with high native cover (>50 %), habitat availability was affected only by the amount of vegetation cover per se, independently of species' dispersal abilities, in accordance with the predictions of the Fragmentation Threshold (Andr n 1994) and the Regime Shift models (Pardini et al. 2010). In such landscapes, patches are generally large and close to each other (Andr n 1994), thus a great part of the landscape remains functionally connected because species only need to cross short distances in the

**Table 1** Performance of 24 models predicting habitat availability across a gradient of native cover in the state of the Rio de Janeiro, Brazil

>50 %			50–30 %			30–10 %			<10 %		
Model	$\Delta_i$	$w_i$	Model	$\Delta_i$	$w_i$	Model	$\Delta_i$	$w_i$	Model	$\Delta_i$	$w_i$
(a) Dispersal ability = 10 m											
NC	0.00	0.45	NC + NP	0.00	0.81	NC + NP	0.00	1.00	NC + PS	0.00	1.00
NC + PI	0.64	0.33	NC + PI	3.18	0.16	NC + PS	71.42	<0.01	NC + NP	44.08	<0.01
NC + PS	2.71	0.12	NC + PS	6.52	0.03	NC + PI	96.50	<0.01	NC + PI	140.78	<0.01
NC + NP	2.80	0.11	NC	20.29	<0.01	NC	132.66	<0.01	NC	142.87	<0.01
(b) Dispersal ability = 50 m											
NC	0.00	0.51	NC + NP	0.00	0.86	NC + NP	0.00	1.00	NC + PS	0.00	1.00
NC + PI	1.78	0.21	NC + PI	3.92	0.12	NC + PS	67.21	<0.01	NC + NP	39.63	<0.01
NC + NP	2.44	0.15	NC + PS	7.54	0.02	NC + PI	88.85	<0.01	NC + PI	143.80	<0.01
NC + PS	2.75	0.13	NC	19.20	<0.01	NC	126.68	<0.01	NC	145.91	<0.01
(c) Dispersal ability = 200 m											
NC	0.00	0.48	NC + NP	0.00	0.94	NC + NP	0.00	1.00	NC + PS	0.00	1.00
NC + NP	1.61	0.21	NC + PI	5.65	0.06	NC + PS	50.55	<0.01	NC + NP	30.54	<0.01
NC + PS	1.89	0.19	NC + PS	9.70	0.01	NC + PI	73.70	<0.01	NC + PI	154.12	<0.01
NC + PI	2.66	0.13	NC	17.15	<0.01	NC	109.30	<0.01	NC	155.46	<0.01
(d) Dispersal ability = 500 m											
NC	0.00	0.50	NC + NP	0.00	0.89	NC + NP	0.00	1.00	NC + PS	0.00	1.00
NC + NP	1.90	0.19	NC + PI	4.45	0.10	NC + PS	27.86	<0.01	NC + NP	33.80	<0.01
NC + PS	1.97	0.19	NC + PS	8.69	0.01	NC + PI	50.87	<0.01	NC + PI	139.50	<0.01
NC + PI	2.76	0.13	NC	13.89	<0.01	NC	82.72	<0.01	NC	139.55	<0.01
(e) Dispersal ability = 1000 m											
NC	0.00	0.54	NC + NP	0.00	0.79	NC + NP	0.00	1.00	NC + PS	0.00	1.00
NC + NP	2.32	0.17	NC + PI	3.01	0.18	NC + PS	12.64	<0.01	NC + NP	30.38	<0.01
NC + PS	2.40	0.16	NC + PS	6.97	0.02	NC + PI	32.13	<0.01	NC + PI	78.66	<0.01
NC + PI	2.78	0.13	NC	10.46	<0.01	NC	58.82	<0.01	NC	79.40	<0.01
(f) Dispersal ability = 3000 m											
NC	0.00	0.57	NC + NP	0.00	0.67	NC + PS	0.00	0.66	NC + PS	0.00	1.00
NC + NP	2.75	0.14	NC + PI	2.00	0.25	NC + NP	1.37	0.34	NC + NP	29.16	<0.01
NC + PI	2.79	0.14	NC + PS	5.22	0.05	NC + PI	14.37	<0.01	NC	53.03	<0.01
NC + PS	2.79	0.14	NC	5.96	0.03	NC	26.77	<0.01	NC + PI	54.35	<0.01

Analyses were carried out separately for six species varying in dispersal ability (10, 50, 200, 500, 1000 or 3000 m) within four scenarios of native cover (>50, 50–30, 30–10, <10 %).  $AICc$  Akaike information criterion corrected for small ratio sample size/number of parameters,  $\Delta_i = AICc_i - \text{minimum } AICc$ ,  $w_i$  Akaike weight,  $NC$  percentage of native cover,  $NP$  number of patches,  $PS$  patch size,  $PI$  patch isolation

matrix. Consequently, such landscapes may have high habitat availability even for species with limited dispersal abilities, potentially sustaining large population sizes (Fahrig 2003) and species richness (Pardini et al. 2010; Martensen et al. 2012).

At the other extreme, when native cover was very low (<10 %), habitat availability for all species was also dependent on patch sizes. In such landscapes,

patch isolation is so high that the variation in isolation values does not have detectable effects on habitat availability, even for the more mobile species. Thus, the amount and proximity of remaining habitat is so low that habitat availability is substantially incremented only through increases in patch sizes. In other words, the intra fraction dominates the values of habitat availability in this scenario (see Saura and

Rubio 2010). The stronger effects of patch size at very low habitat levels support the predictions of the Fragmentation Threshold model (Andr en 1994), but apparently are in disagreement with predictions of the Regime Shift model (Pardini et al. 2010). This apparent discrepancy probably reflects the different response variables considered, habitat availability (our study) versus abundance and richness in Pardini et al. (2010). Habitat availability may change continuously with habitat loss, but species persistence is more likely to exhibit thresholds in habitat amount, below which the population cannot sustain itself even though some habitat is available (With and King 1999; Fahrig 2001, 2003).

In landscapes with intermediate (50–30 %) and low (30–10 %) native cover, the number of patches, in addition to NC, was the main determinant of habitat availability for almost all species. Based on the Fragmentation Threshold and the Regime Shift models, we had expected strong effects of patch size and isolation in these landscapes, but such effects were restricted to the more mobile species (see next paragraph). In landscapes with less than 50 % of native cover, the number of patches was always positively related to patch isolation and negatively related to patch size (see “Methods”). For this reason, the number of patches is likely to combine both patch size and isolation in a single metric, being a more plausible factor than either patch size or isolation alone. Most previous studies of habitat fragmentation ignored the potential effects of the number of patches on biodiversity, focusing only on the size and isolation of patches. This is probably due to the great influence of the Theory of Island Biogeography (MacArthur and Wilson 1967) on landscape ecology, and to the focus of researchers on the patch rather than the landscape scale to assess fragmentation effects (Fahrig 2003). Pardini et al. (2010) detected patch size effects in landscapes with 30 % of native vegetation cover, and suggested that the appearance of such effects may indicate the beginning of a regime shift in biodiversity. Based on our findings, the negative effect of the number of patches can also be considered a warning signal for potentially dangerous fragmentation effects, which can already be recognized in landscapes with native vegetation cover as high as 50–30 %. Such effects are exemplified by Martensen et al. (2012), who documented the higher loss of bird specialist species at landscapes with 50–30 % of forest cover.

Habitat availability increased as species' dispersal abilities increased, in accordance with Saura and Rubio (2010). Despite this, the different species were usually affected by the same set of landscape attributes, although to different extents as mentioned previously. This was clearly the case for landscapes with high (>50 %) native cover, when all species were affected only by native cover, and for landscapes with very low (<10 %) cover, when all species responded to native cover in addition to patch size. In the remaining landscapes, all species responded to native cover in addition to number of patches, but the more mobile species (3000 m) also responded to patch isolation in landscapes with intermediate cover (50–30 %) and mainly to patch size in landscapes with low cover (30–10 %). The effects of patch isolation are evident only for this species in landscapes with intermediate native cover (50–30 %) probably because its dispersal ability (3000 m) is similar to the mean distance among all patches in such landscapes (3350.13 SD  $\pm$  1233.63 m). This mean distance is higher than the dispersal abilities of the other species ( $\leq$ 1000 m), which are thus less likely to be affected directly by patch isolation. The effects of patch size on the more mobile species, in landscapes with low cover (30–10 %), probably reflect the high contribution of the flux fraction of the *PC* index; this contribution generally increases as dispersal abilities of species increase (Saura and Rubio 2010). Because the more mobile species can reach most patches, their sizes are the main determinant of the amount of flux they receive, thus strongly affecting habitat availability. It is important to remember that dispersal abilities are usually correlated with other functional traits of species, especially home range, geographic range size and body size (Whitmee and Orme 2013), which affect minimum area requirements and functional connectivity (Henle et al. 2004; Vetter et al. 2011), potentially impacting habitat availability.

#### Implications for conservation and restoration

Our results indicate that the effectiveness of different management actions is likely to vary depending on the amount of native vegetation cover in the landscape, as proposed previously (Gardner et al. 2009; Pardini et al. 2010). Specifically, management actions intended to increase the number, size or proximity of habitat patches will probably vary in their effects on habitat

availability, depending on the amount of native vegetation cover in the landscape. This is a critical finding given that the resources for conservation are always limited and should be allocated using the best strategy (Sarkar and Illoldi-Rangel 2010; Crouzeilles et al. 2013). Our analyses also suggest that, for a given amount of habitat, species with different dispersal abilities will respond in a same direction, although to different extents, by modifications in a given attribute of landscape configuration, potentially facilitating decision making.

In landscapes with high native cover, conservation efforts should be directed to maintaining what is left, especially by implementing large reserves. We need to retain within landscapes as much native vegetation as possible to guarantee a high and similar amount of available habitat for species with different dispersal abilities. In such landscapes, restoration actions should receive less priority, because it is more efficient to prevent rather than to repair the effects of habitat loss and fragmentation (Rodrigues et al. 2009). For landscapes with less than 50 % of native vegetation cover, conservation actions must be complemented with restoration actions. In landscapes with intermediate and low native cover, restoration should focus on reconnecting habitat patches to reduce their number and isolation (also indirectly increasing their mean size), thus reducing fragmentation levels and increasing habitat availability. This could be achieved, for example, through the creation of habitat corridors (Chetkiewicz et al. 2006). Such actions are fundamental because the effectiveness of management interventions is probably higher in landscapes with around 30 % of native vegetation cover (Pardini et al. 2010). In landscapes with very low native cover, the focus should be on habitat restoration to increase the amount of cover at the landscape scale. Managers must attempt to enlarge patches to increment habitat availability, allowing larger populations to be maintained within patches, thus reducing the chance of local extinction (Bender et al. 1998; Bowman et al. 2002).

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