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The Conservation Value of Small Fragments For Atlantic Forest Reptiles

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ABSTRACT

Loss and fragmentation of natural habitats are key contributors to the decline of populations and impoverishment of biological communities. The response to these disturbances can vary substantially among taxa and depends on spatial metrics of habitat fragments and the surrounding landscape. Herein we test how fragment area, shape, isolation, and matrix quality affect reptile richness, abundance, and occurrence in Brazilian Atlantic Forest fragments, a biodiversity hotspot with a poorly studied reptile fauna. We used 23 forest fragments, ranging from 2 to 30 hectares, surrounded by different matrix types, including sugarcane crop fields, cattle ranching, subsistence farmlands and rural communities. Species richness, total reptile abundance, population abundance, and occurrence probability of many species decreased with fragment area. Model selection suggested that fragment area is the main predictor of both richness and abundance, but matrix quality as well as fragment shape are also important predictors. For population abundance and occurrence probability, fragment area and proximity were the most important predictors followed by fragment shape and matrix quality, but the strength and even the sign of predictors varied substantially among species. We highlight that the value of small fragments should not be neglected for the conservation of Atlantic Forest reptiles.

Abstract in Portuguese is available with online material.

Key words: abundance; habitat fragmentation; matrix quality; occurrence; patch size; proximity; richness and shape.

Habitat loss and fragmentation are key threats to biodiversity, generally leading to population decline and community simplification (Pimm *et al.* 1995, Fahrig 2003). The response of a given taxa to habitat loss and fragmentation depends on fragment (local scale) and landscape (regional scale) features, as well as intrinsic ecological traits of the taxa (Turner 2005).

Fragment size and shape are traditionally used as local-scale metrics implicated in the dynamics of communities and populations in isolated fragments (Martinez-Morales 2005, Benchimol & Peres 2013, Garmendia *et al.* 2013). Fragment size is frequently assumed to be positively correlated with habitat quality, while more irregularly shaped and smaller fragments are more affected by edge effects and considered to be of lower quality. Therefore, it is expected that smaller fragments will support fewer individuals and species because they contain fewer habitats/resources.

Landscape features also influence fragment quality. The degree of isolation of a given fragment from a single large habitat remnant was considered a key landscape metric in MacArthur and Wilson's Island Biogeography Theory (1967). Isolated fragments have a lower probability of colonization and, in general, are considered of inferior quality. The development of complex metrics allow us to integrate the area and isolation of multiple habitat remnants in relation to a given focal fragment, incorporating landscape configuration into a single fragmentation metric (Gustafson & Parker 1992). Furthermore, recent studies indicate that the quality of the matrix itself (formerly considered simply as non-habitat) has a strong influence on the maintenance of fragmented populations (Vandermeer & Carvajal 2001, Fahrig 2002, Kupfer *et al.* 2006, Prugh *et al.* 2008, Umetsu *et al.* 2008). From this perspective, the landscape is composed of diverse elements of land cover, varying in size, shape, and quality.

Despite the general expectations related to fragment size, shape, isolation, and matrix type, response to habitat fragmentation is highly taxon-dependent because different species perceive the environment in different ways (Gascon *et al.* 1999, Driscoll 2004, Pardini *et al.* 2009). Furthermore, unexpected outcomes can emerge because local abiotic conditions and ecological processes such as competition, predation, and dispersal are altered as a result of fragmentation (Murcia 1995, Ries *et al.* 2004). In fact, the general response of a given taxon to fragmentation can hide a high degree of heterogeneity within that taxon. For instance, the influence of matrix composition on the dynamics of populations isolated in fragments can be species-specific (Atauri & de Lucio 2001, Prevedello & Vieira 2010). Generalist species can occur almost equally in different matrix types (Gascon *et al.* 1999, Dixo & Metzger 2009, Pardini *et al.* 2009), while some species can thrive in specific matrix categories but are strongly suppressed by others (Brosi *et al.* 2008, Hansbauer *et al.* 2010).

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Global extinction threat levels for reptiles (20%) are higher than for birds (13%) and only slightly lower than for mammals and freshwater fishes (25%) (Bohm *et al.* 2013). However, less attention has been given to reptiles in the literature in comparison to other vertebrates (Gibbons *et al.* 2000, Foster *et al.* 2012), while species description rates continue to accelerate (Uetz 2010). Research on the effects of landscape fragmentation on vertebrates is skewed toward birds, mammals, and amphibians (Mac Nally & Brown 2001). Moreover, information about threats to reptiles has been mostly generated by studies in temperate regions (Gardner *et al.* 2007).

Reptiles have lower energy requirements, smaller home ranges, and higher densities compared to homeothermic animals of the same size (Pough 1980), which might allow their persistence even in small areas (McGarigal & Cushman 2002). At the same time, reptiles have relatively low dispersal abilities, experience thermoregulatory constraints and often are specialized on a substrate type, which leads to greater sensitiveness to habitat alteration (Kearney *et al.* 2009). Studies on reptiles have found both adverse effects (Alcala *et al.* 2004, Dixo & Metzger 2009, Williams *et al.* 2012) and neutral/positive effects in response to fragmentation (Bell & Donnelly 2006, Schutz & Driscoll 2008, Rubio & Simonetti 2011, Cabrera-Guzmán & Reynoso 2012), depending on the species studied and the metric used. Furthermore, most studies recognize that species-specific traits are important for particular responses to fragmentation (Pardini *et al.* 2009, Cabrera-Guzmán & Reynoso 2012, Williams *et al.* 2012).

This study tested how fragment area, shape, isolation, and matrix quality affect the richness, abundance, and occurrence of reptiles in the Brazilian Atlantic Forest, a biodiversity hotspot with a poorly studied reptile fauna (Myers *et al.* 2000, Rodrigues 2005). We also performed a systematic literature review to describe the generality of area, shape, isolation, and matrix quality effects on squamates around the world. In principle, we expected that smaller, isolated fragments with more edge and surrounded by lower quality matrices would be more depauperate in species and individuals. However, we also expected some degree of heterogeneity among the species because of their different ecological traits.

METHODS

Study area.—The study was conducted at the extreme northeastern portion of the Brazilian Atlantic Forest (Fig. 1). About 11.73 percent of the original Atlantic Forest cover persists today and 83.4 percent occurs in fragments smaller than 50 ha (Ribeiro *et al.* 2009). Northeastern Atlantic Forest is a tropical forest with evergreen and semi-deciduous physiognomies, but due to long-term fragmentation process and, consequently edge effects, is characterized by impoverished tree communities (Santos *et al.* 2008). In our study landscape, there are 278 small forest fragments, 80.2 percent smaller than 50 ha. The regional climate is seasonal tropical with a rainy period concentrated between March and July, and mean rainfall of 1284 mm/yr (EMPARN 2012).

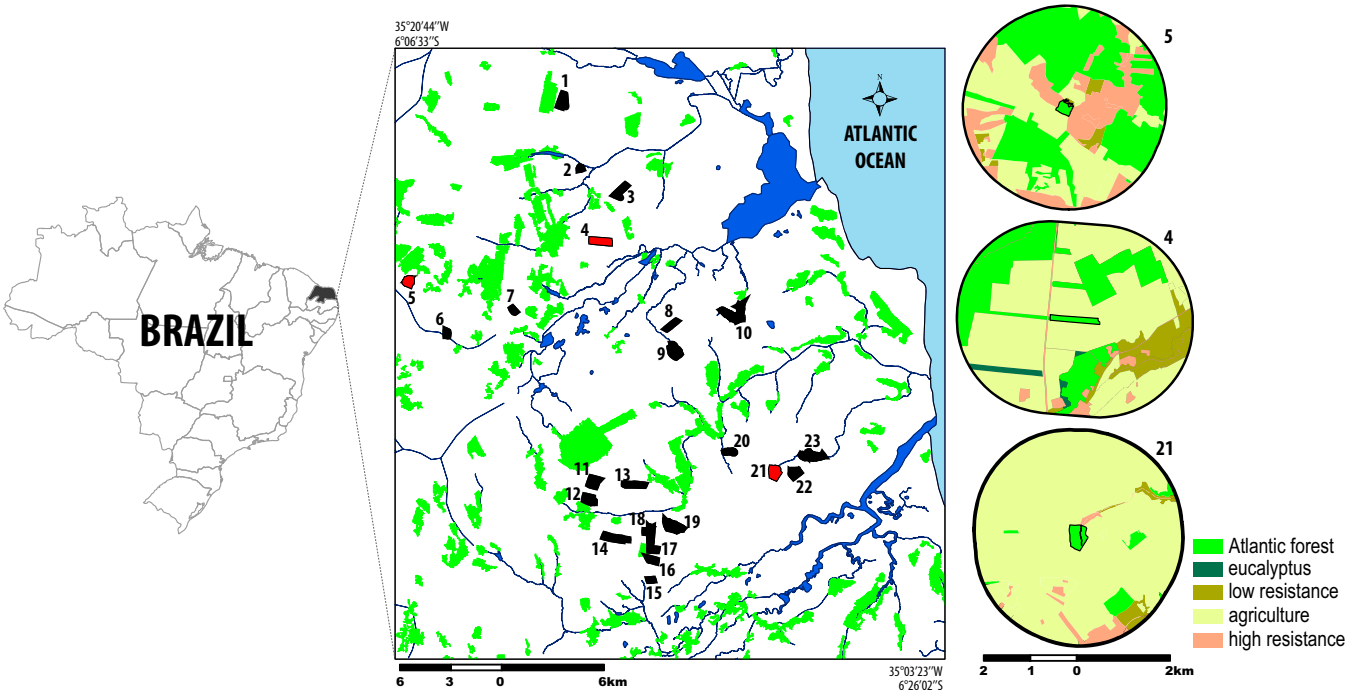

FIGURE 1. Study landscape showing the 23 sampled fragments in black. The three red ones exemplify fragments with classified buffers in the right side, which present increasing lost of forest cover on matrix: (5) high forest cover, (4) intermediate, and (21) low forest cover.

Most of the Brazilian human population currently lives in the area originally occupied by the Atlantic Forest (IBGE 2010). Consequently, the remaining forest fragments are frequently embedded in anthropogenic matrices that vary in quality and include secondary forests, forestry stands, agricultural areas, cattle ranches, abandoned fields, roads, and cities. In the Brazilian northeast, as well as in our study landscape, the forest fragments are commonly embedded in sugarcane plantations used in sugar and ethanol production.

Sampling design.—We built a landscape map in ArcGIS v.9.3 (ESRI) based on aerial photographs (5 m resolution, year 2003), forest cover provided by the NGO SOS Mata Atlântica, high-resolution Google Earth imagery, and field observations. From an area of 1166 km^2 (Fig. 1), we selected 23 forest fragments that ranged in size from 1.7 to 27.4 ha. We selected fragments surrounded primarily by sugarcane plantations. We also selected scattered fragments of different sizes to avoid spatial autocorrelation. After data collection, we tested for spatial autocorrelation using the software Spatial Analysis in Macroecology—SAM (Rangel *et al.* 2010) and confirmed that full regression model residuals (for species richness and abundance) were not spatially autocorrelated (Moran's I; $P > 0.05$). Therefore, subsequent analyses did not control for spatial effects.

In each fragment, we installed three pitfall trap arrays (spaced 20 m apart), each composed of three 60 L buckets (40 cm of diameter and 48 cm deep) connected by 6 m drift fences. The central bucket was positioned at the fragment centroid. We sampled during the wet season, from May to July 2011. Each fragment was sampled 7 days per month in a 3-mo period, totaling 21 sampling days per fragment. Thus, sampling effort was the same in all sites, regardless of fragment size. Although secretive and habitat specific species may be underrepresented in this sampling design, this standardization allowed us to directly compare fragments avoiding the confounding effects of species–area relationship and area sampled (see Fahrig 2013).

In total, our sampling effort was 4077 trap nights due to some missing traps. Three specimens per species were collected as vouchers, and all remaining animals caught in traps were marked individually by toe-clipping and released. We only considered the first capture of individuals in the analyses.

We performed a qualitative systematic literature review using the Web of Science platform. The following search algorithm was applied: TOPIC: (lizard* OR snake* OR reptile* OR herpetofauna OR squamat*) AND TOPIC: ('habitat fragmentation' OR 'reserve size' OR 'patch size' OR 'forest fragmentation' OR 'fragmented landscape*'). We searched the literature up to year 2014 for studies that tested fragment size, shape, isolation, and/or matrix quality as predictors of species richness, abundance, occurrence, and indicators of species demography or genetic diversity. We included only case studies with squamate species. We did not include reviews, computer simulations or modeling, studies that only evaluate genetic structure or community structure and biogeographic implications, or research on habitat restoration.

Analyses.—Spatial landscape metrics were generated in ArcGIS v.9.3 and Fragstats 4.1 (McGarigal *et al.* 2012). We considered two local-scale metrics and two landscape-scale metrics as predictors of species richness, occurrence, and abundances in fragments. Fragment area (AREA; in hectares) and shape were the local-scale metrics, directly extracted from fragments. We used the *Shape Index* (SHAPE) implemented in Fragstats to estimate fragment shape complexity, following the formula: $SHAPE = 0.25P_i/\sqrt{a_i}$, where: P_i = perimeter of fragment i (m), and a_i = area of fragment i (m^2) corrected by a constant to adjust for a square standard. This metric describes the proportion of patch edge relative to patch size, minimizing the correlation between shape and size. Greater values of this index indicates fragments with more complex shape and consequently with higher proportion of edge.

For the landscape-scale metrics, we classified land cover inside a buffer of 2 km around fragments. We estimated a structural metric, the *Proximity Index* (PROX), and a functional metric, the *Matrix Quality* (MATRIX). PROX estimates the degree of isolation and intensity of fragmentation for each focal fragment by the formula:

$$\text{PROX} = \sum_{s=1}^{n} a_j / h_{ij}^2$$

where: a_j = area of fragment j (m^2) inside specified radius (m) from focal fragment i; and h_{ij} = edge-to-edge distance (m) between focal fragment i and fragment j, inside a specified radius (m). PROX values were positively correlated with the proportion of forest inside the buffer zones $r = 0.52$, $P = 0.0115$. Greater values of PROX indicate a less isolated fragment and a less fragmented landscape (Gustafson & Parker 1994).

For the matrix quality (MATRIX) metric, land cover classes were collapsed into four classes according to intensity of human use and matrix resistance for reptiles (Fig. 1). We assigned quality scores (Qi) for these classes (in each fragment 2 km buffer zone) based on our previous experience and observations: I—high resistance (0.2; houses, industry, pasture, roads, bare soil, shrimp farming, river and lake), II—agriculture (0.3; sugarcane, small farmlands, and coconut fields), III—low resistance (0.6; abandoned field and marsh), and IV—eucalyptus forest (0.9). We excluded the category 'forest' from MATRIX estimative to avoid correlation with PROX metric. Therefore, our matrix quality estimate considered all the land uses surrounding fragments that were 'non-habitat'. Matrix quality was calculated as the weighted average of matrix quality scores based on the percentage of each land cover (plandi) according to the expression: $BMQ = \sum plandiQi/\sum plandi$. Greater values of MATRIX indicate a less altered landscape.

We used multiple regression models to test how species richness, total abundance, abundance of each species, and species occurrence were affected by fragments area and shape, proximity and matrix quality in buffers. In the population analyses, which predicted species occurrences and abundances, we only used the

five species that had ten or more individuals captured and five or more occurrences. The predictor variables were not significantly correlated ($P > 0.05$ for Pearson correlation with Bonferonni correction). In total, we considered 16 additive models, including the minimal model (no explanatory variables), four single factor models (AREA, SHAPE, PROX, and MATRIX), and 11 models considering all combinations of the four factors. Given that species richness and abundance are count data, the models assumed Poisson error distributions. Because we detected overdispersion in our data and our sample size was modest, model selection used the QAICc criterion, implemented in the package Bbmle in R (Bolker 2013). Due to convergence difficulties, presence/absence of each species in fragments was modeled using Bayesian logistic regression as implemented by Arm package in R (Gelman & Hill 2007). We accepted models with ΔQAICc ≤ 2 (Burnham & Anderson 2002).

RESULTS

Community.—We captured a total of 192 individuals belonging to 15 squamate species (Table S1; Fig. 2). Marked individuals were never recaptured in fragments other than the ones in which they were originally caught. Most individuals captured in fragments belong to species associated with leaf litter forest environments (155 individuals or 81%; Table S1). Given that number of snakes captured was too low (ten individuals in six species; Table S1), snakes were considered only in fragment's community evaluations and not in population analysis. Despite our limited sampling time and therefore a relatively low number of individuals collected, our results are within the upper values of richness and abundances recovered for the Atlantic Forest using pitfall traps: second for richness and third for abundance compared to other seven sites available in the literature (see table 3 in Almeida-Gomes & Rocha 2014).

Fragment area was the only significant landscape variable affecting reptile richness in simple regressions (βstd = −0.247, t = −3.585, P = 0.002, r^2 = 0.371; Fig. 3A). Based on ΔQAICc model averaging, AREA was the most important variable explaining richness (RI = 1), but MATRIX was also selected (RI = 0.415; Table 1). Unexpectedly, the area coefficient was negative, indicating that smaller fragments had more reptile species. However, MATRIX coefficient was positive (Fig. 3G).

AREA was also the only significant predictor affecting total species abundance in simple regressions (βstd = −0.372, t = −3.986, P = 0.001, r^2 = 0.451; Fig. 3B) and was the variable with greatest importance in model averaging (RI = 1; Table 1). SHAPE was also important for total species abundance (RI = 0.698), but with a positive coefficient. Removal of an outlier for SHAPE (fragment 10 in Fig. 1) did not change qualitatively the results: both AREA and SHAPE remained the only selected variables.

Populations.—The three most abundant species, *Dryadosaura nordestina* (N = 80), *Kentropyx calcarata* (N = 33), and *Enyalius bibronii* (N = 27), showed similar responses to the fragments' characteristics: AREA and PROX were both selected in the best models explaining number of individuals captured. Abundance of these three species had a negative relation with AREA and a positive relation with PROX in all models selected (Table 2).

For *Tropidurus hispidus* (N = 24), a single best model was selected, including AREA + SHAPE + PROX (ΔQAICc = 0; W_i = 1; r^2 = 0.601). Simple linear regression indicated that AREA was marginally significantly associated with species abundance (βstd = −1.211, t = −2.059, P = 0.052, r^2 = 0.315). AREA and PROX were both negatively related to species abundance, while SHAPE was positively related to abundance (Table 2).

Lastly, *Coleodactylus natalensis* (N = 10) had two alternative models accepted. The first contained AREA + SHAPE + PROX (ΔQAICc = 0; W_i = 0.5 46; r^2 = 0.725), and the second contained all variables tested AREA + SHAPE + PROX + MATRIX (ΔQAICc = 0.369; W_i = 0.454; r^2 = 0.764). For this species, PROX was the only significant variable in simple regressions and, contrary to expectation, the slope coefficient was negative (βstd = −1.871, t = −3.284, P = 0.004, r^2 = 0.531).

Occurrence.—Three selected models influenced *D. nordestina* ($N_{occurrences}$ = 20) occurrence in fragments: minimal (ΔQAICc = 0; W_i = 0.505), PROX (ΔQAICc = 1.286; W_i = 0.265), and AREA (ΔQAICc = 1.573; W_i = 0.230; averaged model for all species are presented in Table 2). For *K. calcarata* ($N_{occurrences}$ = 14), two models were selected: minimal (ΔQAICc = 0; W_i = 0.640) and PROX (ΔQAICc = 1.150; W_i = 0.360). For *E. bibronii* ($N_{occurrences}$ = 13), PROX was significantly related to occurrences in fragments (βstd = 1.111, t = 2.092, P = 0.037), and four models were selected: PROX (ΔQAICc = 0; W_i = 0.363), PROX+MATRIX (ΔQAICc = 0.689; W_i = 0.278), AREA+PROX (ΔQAICc = 1.531; W_i = 0.183), and SHAPE+-PROX (ΔQAICc = 1.968; W_i = 0.147). AREA significantly affected the occurrence of *T. hispidus* ($N_{occurrences}$ = 9) in fragments (βstd = −1.134, t = −2.158, P = 0.031) and three models were selected: AREA (ΔQAICc = 0; W_i = 0.461), AREA + SHAPE (ΔQAICc = 0.511; W_i = 0.357), and AREA+PROX (ΔQAICc = 1.850; W_i = 0.183). PROX was significantly related to the occurrence of *C. natalensis* ($N_{occurrences}$ = 5) in fragments, but with a negative coefficient (βstd = −2.009, t = −2.245, P = 0.025) and four models were selected: PROX (ΔQAICc = 0; W_i = 0.417), PROX + MATRIX (ΔQAICc = 1.264; W_i = 0.222), SHAPE + PROX (ΔQAICc = 1.633; W_i = 0.184), and AREA+PROX (ΔQAICc = 1.713; W_i = 0.177).

We found 33 studies that evaluated AREA, SHAPE, PROX, and/or MATRIX as predictors of species richness, abundance, occurrence, and indicators of species demography or genetic diversity (Table S2). Most studies recorded a positive effect of AREA on species diversity indicators (N = 16), some show no effect (N = 13), and a few (N = 3) recovered negative effects. Two studies found no effect of SHAPE, two found a negative effect on species diversity indicators, and one found a positive

FIGURE 2. Species captured in the study: *Dryadosaura nordestina* (A), *Kentropyx calcarata* (B), *Enyalius bibronii* (C), *Tropidurus hispidus* (D), *Coleodactylus natalensis* (E), *Ameiva ameiva* (F), *Lygodactylus klugei* (G), *Anolis* cf *fuscoauratus* (H), *Mabuya macrorhyncha* (I), *Micrurus corallinus* (J), *Micrurus ibiboboca* (K), *Tantilla melanocephala* (L), *Typhlops brongersmianus* (M), *Taeniophallus occipitalis* (N), *Xenodon merremi* (O—photo by W. Pessoa).

effect. Most studies found no effect of isolation (the opposite of PROX) on species diversity indicators ($N = 10$), and while a few found negative effects ($N = 7$) no study recovered a positive effect of this metric on reptile communities. MATRIX presented a positive effect on species diversity indicators in every case for which it was tested ($N = 7$).

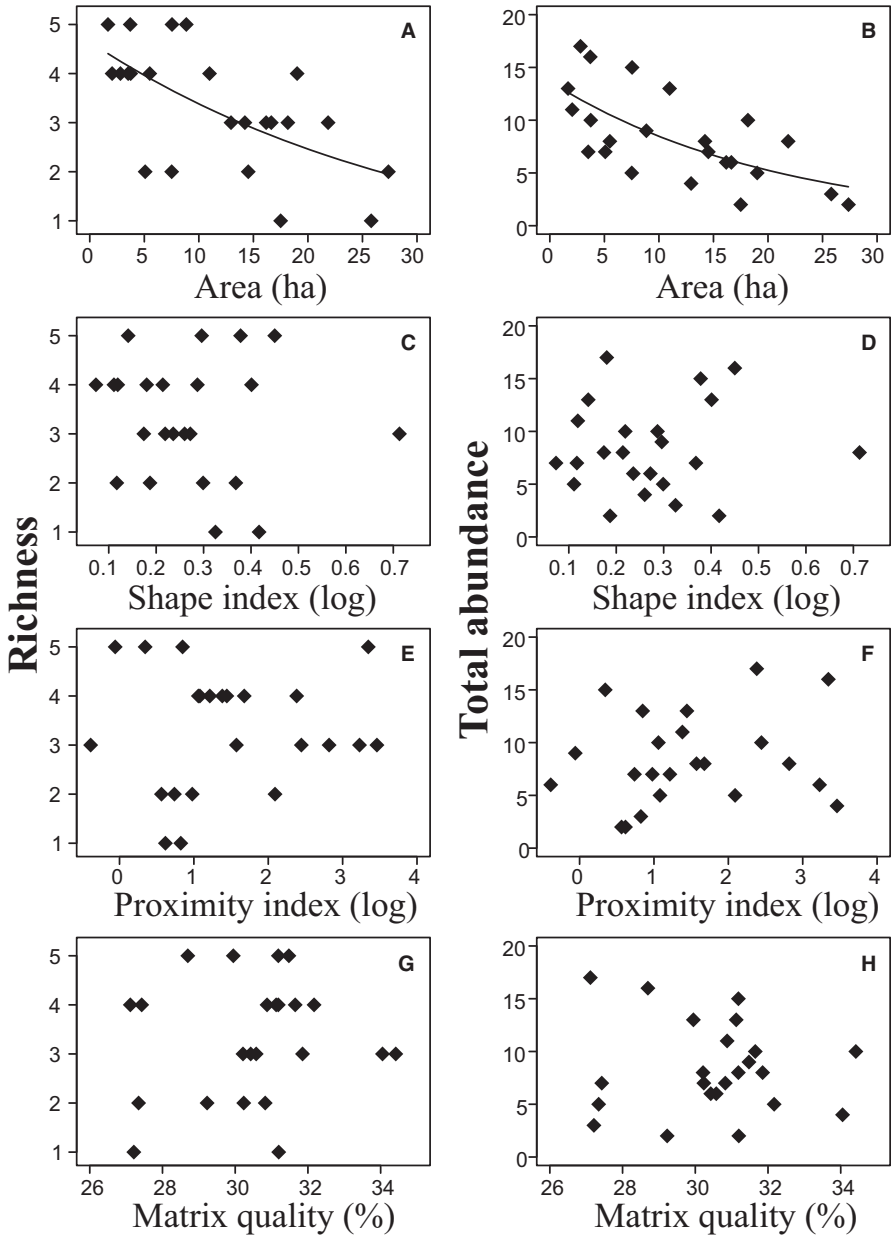

FIGURE 3. Simple regressions for richness (left) and abundance (right) considering the four predictors tested: fragment area (A) βstd = −0.247, t = −3.585, P = 0.002, r^2 = 0.371 and (B) βstd = −0.372, t = −3.986, P = 0.001, r^2 = 0.451; fragment shape (C) βstd = −0.043, t = −0.521, P = 0.608, r^2 = 0.012 and (D) βstd = 0.036, t = 0.335, P = 0.741, r^2 = 0.005; fragment isolation (E) βstd = 0.022, t = 0.270, P = 0.790, r^2 = 0.003 and (F) βstd = 0.091, t = 0.849, P = 0.405, r^2 = 0.032; and matrix quality (G) βstd = 0.046, t = 0.571, P = 0.574, r^2 = 0.014 and (H) βstd = −0.039, t = −0.352, P = 0.728, r^2 = 0.006.

DISCUSSION

Fragment and landscape features affected the richness and total abundance of reptiles in isolated forest fragments, highlighting the importance of local and landscape-scale spatial processes. Fragment area and the quality of the surrounding matrix were the two main factors affecting species richness, while fragment area and shape were the two main factors affecting total reptile abundance. Interestingly, contrary to expectations from metapopulation models (Hanski & Gilpin 1991, Bender *et al.* 2003), proximity did not influence community attributes. The population approach also revealed that fragment and landscape features are relevant for species survival in fragmented landscape. However, the results clearly show that the effect of different metrics on richness, abundance, and occurrence is species-specific.

Contrary to theoretical expectations (MacArthur & Wilson 1967, Hanski 1998), richness and total abundance of reptiles were not positively related to fragment size. Furthermore, population

TABLE 1. *Models selected according QAIC criteria (ΔQAICc < 2) for richness and abundance. The averaged model is presented with the mean coefficient and relative importance for each predictor selected (AREA, MATRIX, SHAPE, or PROX). The number of parameters (k), regression coefficients (β), difference of QAIC values corrected for small sample sizes (ΔQAICc), Akaike Weights (W_i), and percentage of deviance explained by each model (%DE) are also presented for selected models.*

Models	*k*	AREA (*β*)	SHAPE (*β*)	PROX (*β*)	MATRIX (*β*)	ΔQAICc	W_i	%DE
Richness								
Area	2	−0.247 ± 0.069*	–	–	–	0	0.585	0.371
Area + Matrix	3	−0.276 ± 0.071*	–	–	0.104 ± 0.067	0.688	0.415	0.435
β mean		−0.259 ± 0.071	–	–	0.043 ± 0.062			
Relative importance		1	–	–	0.415			
Total abundance								
Area + Shape	3	−0.447 ± 0.094*	0.184 ± 0.082*	–	–	0	0.698	0.557
Area	2	−0.372 ± 0.093*	–	–	–	1.68	0.302	0.451
β mean		−0.425 ± 0.100	0.129 ± 0.108	–	–			
Relative importance		1	0.698	–	–			

*$P < 0.05$ in simple or multiple regression according to selected model showed in first column.

TABLE 2. *Averaged models for species abundance and occurrence in fragments (ΔQAICc < 2). Only species with ten or more captures in five or more fragments were considered. For each predictor, the mean coefficient and relative importance (in parenthesis) are shown.*

	AREA	SHAPE	PROX	MATRIX
Population abundance				
Dryadosaura nordestina	−0.023 ± 0.051 (0.195)	–	0.047 ± 0.083 (0.285)	–
Kentropyx calcarata	−0.116 ± 0.199 (0.300)	–	0.090 ± 0.162 (0.272)	–
Enyalius bibronii	−0.277 ± 0.366 (0.482)	–	0.189 ± 0.274 (0.421)	–
Tropidurus hispidus	−2.415 ± 0.684# (1)	1.011 ± 0.372 (1)	−0.971 ± 0.316 (1)	–
Coleodactylus natalensis	−0.799 ± 0.386 (1)	−1.430 ± 0 .704 (1)	−3.117 ± 0.738* (1)	0.444 ± 0.597 (0.454)
Species occurrence				
Dryadosaura nordestina	−0.093 ± 0.209 (0.230)	–	0.133 ± 0.277 (0.265)	–
Kentropyx calcarata	–	–	0.153 ± 0.278 (0.360)	–
Enyalius bibronii	−0.079 ± 0.167 (0.183)	−0.046 ± 0.111 (0.147)	1.121 ± 0.542* (1)	0.165 ± 0.302 (0.278)
Tropidurus hispidus	−1.252 ± 0.579* (1)	0.206 ± 0.352 (0.357)	−0.063 ± 0.148* (0.183)	–
Coleodactylus natalensis	−0.063 ± 0.153 (0.177)	−0.077 ± 0.188 (0.184)	−2.080 ± 0.920* (1)	0.147 ± 0.304 (0.222)

*$P < 0.050$ and #$P = 0.052$ in simple regressions.

abundance and species occurrence probability of all tested species consistently responded negatively to the increase in fragment size. Results from other studies have shown that reptile communities in forest fragments tend to respond positively to fragment size, with larger fragments harboring more species in greater abundance (Kitchener *et al.* 1980, Smith *et al.* 1996, Mac Nally & Brown 2001). However, this trend is not pervasive and cases of no effect (Diaz *et al.* 2000, Schlaepfer & Gavin 2001, Watling & Donnelly 2008) and negative effects on richness and abundances of reptiles have also been reported (Bell & Donnelly 2006, Schutz & Driscoll 2008, Cabrera-Guzmán & Reynoso 2012). Indeed, we found an equivalent number of publications reporting positive ($N = 16$) compared to no ($N = 13$) or negative ($N = 3$) effects of increasing fragment area on squamate species diversity indicators.

Positive effects of fragment area are expected on several patch attributes, such as resource availability, territory size, habitat quality, and heterogeneity (Kitchener *et al.* 1980, Blevins & With 2011, Garda *et al.* 2013). Explanations for the opposite trend are less straightforward and generally involve *ad hoc* hypotheses (Andersson *et al.* 2010, Cabrera-Guzmán & Reynoso 2012). Greater availability of refuges (*e.g.*, decaying logs, fallen debris: Cabrera-Guzmán & Reynoso 2012), refuge temperatures (Andersson *et al.* 2010), and edge effects (Lehtinen *et al.* 2003, Schutz & Driscoll 2008) have been suggested as possible causes of higher abundances in smaller fragments. For instance, smaller fragments are

more susceptible to edge effects, and a greater proportion of total area is affected by climatic and biotic influences from the surrounding matrix, resulting in modified microhabitats, which can significantly affect the occurrence of lizards in tropical forests (Garda *et al.* 2013).

Fragment edges have been shown to harbor more squamate species at higher densities compared to forest interior (Rubio & Simonetti 2011, Sato *et al.* 2014, Carvajal-Cogollo & Urbina-Cardona 2015). In our study, we sampled only fragment centroids, and in smaller fragments pitfalls were closer to fragments edges. This could have increased the influence of edges in smaller fragments, leading to higher diversities and abundances. Nevertheless, we collected more individuals but not more species in fragments with complex shapes, suggesting that edge effects did not influenced our capture rates. Our systematic review showed that SHAPE as well as AREA have inconsistent effects on reptiles populations and communities in fragmented landscapes (Table S2), and that responses are greatly dependent on species-specific tolerances.

Top-down release is another potential biotic mechanism that may explain the greater richness of reptiles in smaller fragments. As fragmentation proceeds, smaller fragments are more prone to loss of large, predatory birds than larger fragments (Turner 1996, Sodhi *et al.* 2004). Potentially, these local extinctions can release the predation pressure on small-sized lizards. Birds from Cracidae family (guans), raptors (like *Leptodon forbesi*), and pigmy owls (*Glaucidium mooreorum*) were previously distributed and even common in the study area, but are all currently endangered, some even extinct in the wild (Poulin *et al.* 2001, Pereira & Brooks 2006). It is likely that remaining avian predators are absent from smaller fragments, potentially releasing lizard species from the predation pressure by these animals. Top-down release can also be due to parasites. There is evidence that parasite infection is reduced in lizards captured at fragment's edge compared to fragment's interior (Schlaepfer & Gavin 2001). Because smaller fragments have a higher edge to center ratio, in principle, they could sustain smaller parasite populations, elevating the fitness of reptiles in those areas (Main & Bull 2000).

The top-down release hypothesis may partially explain the diversity of community responses to fragmentation found in the literature (*i.e.*, positive, neutral and negative responses), because the hypothesis predicts a U-shape relationship between richness and fragment size. According to this top-down release hypothesis, richness and abundance of reptiles are expected to decline with decreasing fragment size until fragments are too small to maintain viable populations of predator species. After this tipping point, richness and diversity would start to rise due to top-down release (Crooks & Soule 1999, Elmhagen & Rushton 2007). In fact, when we plotted fragment size against squamate richness for 209 fragments from 12 independent studies (Table S3), there was an overall positive relationship (Fig. 4; $\beta = 0.277$, $z = 24.08$, $P < 0.001$). However, when one looks at fragments below several threshold sizes, negative trends are suggested ($\beta_{\leq 1\ ha} = -0.260$, $\beta_{\leq 1.5\ ha} = -0.522$, $\beta_{\leq 2\ ha} = -0.188$, $\beta_{\leq 2.5\ ha} = -0.048$, $\beta_{\leq 3\ ha} = -0.077$).

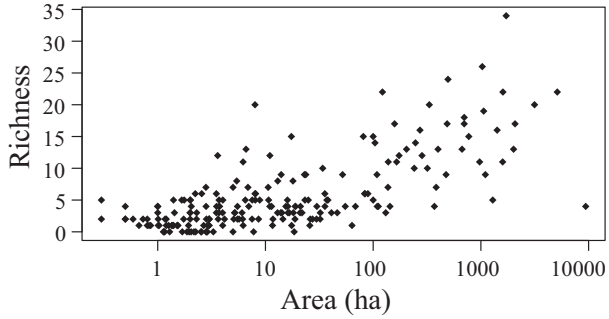

FIGURE 4. Squamate richness plotted against fragment size (in hectares). GLM regression, assuming Poisson error distribution: $\beta = 0.277$, $z = 24.08$, $P < 0.001$. Data compiled from 209 fragments in 12 independent studies (see Table S3).

The top-down release would only apply to forest species. Most individuals we captured (81%) are forest species and, moreover, four of five species with enough captures to enter the population analysis are closely associated with forest environments (Table S1), occurring on the leaf litter (*D. nordestina, K. calcarata, and C. natalensis*) or exhibiting semi arboreal habits (*E. bibronii*). Therefore, the increase in abundances detected in smaller fragments could be a consequence of this mechanism. Greater abundances have been reported in another study of reptiles in fragments up to 7 hectares in size (Cabrera-Guzmán & Reynoso 2012), although this pattern was not observed for richness.

In our study, species common in open areas were more frequently found in smaller fragments, probably due to higher edge proportion and because in these smaller fragments our sample grid was closer to fragments edge. Originally, the Atlantic Forest in Rio Grande do Norte contained patches of open vegetation (called Tabuleiros and Restingas) that harbored open area lizard species, including those from the semi-arid Caatinga scrublands and dry forests (Freire 1996). With the fragmentation process, some of these species were able to colonize smaller fragments. For instance, *Lygodactylus klugei*, a Caatinga endemic (Leal *et al.* 2003), was found only in one small fragment (3.5 ha). *Ameiva ameiva*, a generalist species typical of open biomes such as the savannah-like Cerrado and Caatinga (Sartorius *et al.* 1999), was also found mostly in small fragments (2.1, 3.7, and 19 ha; Table S1).

Only one of five species in the population analysis is not typical of forest habitats: *T. hispidus*, a heliophilic species distributed in open areas in northern and northeastern Brazil (Pianka & Vitt 2003), markedly generalist and commonly found in residential backyards. Accordingly, it was the only species for which fragment area significantly affected occurrence and marginally ($P = 0.052$) abundance. The higher abundance of this sit-and-wait open area forager, compared to the active forager *A. ameiva*, may result from its territorial behavior (Vitt & Caldwell 2009). Once an adequate site with enough light is found within the forest, a small population can be established locally. In contrast, active foragers that do not defend fixed territories wander

from canopy gap to canopy gap (Sartorius *et al.* 1999), not establishing populations within the fragments.

Local and landscape variables influenced the abundances and occurrences of species differently. The PROX variable (the inverse of isolation) appeared in models explaining abundance and occurrence of all five species. For *Coleodactylus natalensis*, PROX was the most important predictor, but with a negative coefficient: more isolated areas had more occurrences and higher abundances. This is one of the world's smallest lizard species, with a mean SVL of 2 cm (Freire 1999). *Coleodactylus natalensis* therefore has limited mobility and is unlikely to exchange individuals between disconnected fragments. Because isolated patches experience greater extinction rates, and larger animals at higher trophic levels are more extinction prone (Gaston & Blackburn 1996, Davies *et al.* 2000, Purvis *et al.* 2000), it is possible that predators may have become extinct in these isolated areas (see above), releasing populations of *Coleodactylus* from this pressure. Although isolation has never been shown to correlate positively with any aspect of reptile diversity, it rarely has the opposite trend, with most studies accessing this metric detecting no influence of isolation on community or population metrics (Table S2).

The other species favored by isolation was *T. hispidus*, but in this case most likely because of its generalist behavior and pervasiveness in the surrounding matrix. In contrast, PROX was positive for *E. bibronii*, *K. calcarata*, and *D. nordestina*, all forest specialists larger than *C. natalensis* and likely benefiting from increased opportunities for migration among fragments. Finally, *E. bibronii* and *C. natalensis* were negatively related to shape complexity (SHAPE) but positively associated with matrix quality (MATRIX), highlighting the specialization of these forest-dependent species on conditions structurally similar to forest environments. Our findings related to matrix quality corroborate results reported in the literature (Table S2), where all studies that accessed this metric recovered a positive influence on reptiles in fragmented landscapes.

Our results indicate that small fragments have high conservation value for reptiles in the Atlantic Forest of Northeast Brazil. The presence of forest reptiles in such small remnants can perhaps be attributed to the absence or, at least, low density of top-predators. If that is the case, a conservation puzzle is in place. How to restore and expand the original habitat of the Atlantic Forest without risking introducing the reptile predators? The implementation of a proper management regime will require more information of such top-down density dependent processes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

TABLE S1. *Study data base presented according to fragments size.*

TABLE S2. *Publications that tested for the relation between at least one of the four predictors used in this study.*

TABLE S3. *Information on fragment sizes (hectares) and squamate richness compiled from 12 studies, plus the present study.*

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