

Metacommunity structure in a highly fragmented forest: has deforestation in the Atlantic Forest altered historic biogeographic patterns?

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ABSTRACT

Aim To determine whether there is evidence of changes in small mammals distributions and emergent metacommunity structure in the Atlantic Forest resulting from extensive habitat loss and fragmentation associated with anthropogenic activities.

Location South American Atlantic Forest from northeastern Brazil to eastern Paraguay.

Methods Using presence–absence data for non-volant small mammals, we analysed metacommunity structure for communities from 76 fragments distributed throughout Atlantic Forest. We evaluated coherence, range turnover and range boundary clumping for the entire non-volant small mammal assemblage, marsupials, rodents and sigmodontine rodents separately. β -diversity based on the multiplicative model was used to estimate the number of compartments (groups of sites with similar species composition) in Clementsian structures, and cluster analysis identified which sites formed compartments. Canonical correspondence analysis determined which environmental factors were associated with the gradients along which metacommunities were structured. Distance-decay analysis evaluated the spatial structure in small mammal and environmental data, and Mantel tests evaluated correlations between them.

Results Rodent metacommunities had Clementsian structure, whereas marsupials had Gleasonian structure. Compartment locations for rodents were consistent with areas of endemism. Temperature seasonality was most associated with the gradients along which metacommunities were structured. Assemblage and environmental dissimilarity among sites had significant positive relationships with geographic distance.

Main conclusions Compartment locations in Clementsian structures mirrored historical refugium locations and important vicariance events associated with large rivers. Despite extensive deforestation in Atlantic Forest, small mammal distributions are consistent with expectations based on historical biogeography, suggesting that anthropogenic activities have not yet greatly affected geographic distributions of emergent metacommunity structures. However, extinction debt associated with recent fragmentation and habitat loss may exist. Any effective conservation plan for large and fragmented biomes must consider areas of endemism to maintain regional biodiversity and maintain sufficiently large and connected fragments to facilitate rescue effects and minimize effects of extinction debt.

Keywords

β -diversity, biodiversity, Clementsian structure, fragmentation, small mammals.

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INTRODUCTION

Metacommunity structure

The metacommunity concept has emerged as an important approach for contemporary studies in community ecology because it explicitly recognizes that both local (e.g. biotic interactions, environmental tolerances) and regional (e.g. dispersal, habitat fragmentation) factors are responsible for the composition of local communities as well as for spatial variation in community composition (Leibold *et al.*, 2004). The increased interest in broad-scale patterns of biodiversity (Ricklefs, 2004; Schipper *et al.*, 2008) and a better understanding of the contribution of regional factors to the assembly of local communities (Belmaker & Jetz, 2012) have changed our perception of a community from that of a localized group of interacting species to one in which the spatial distribution of species has become a greater focus for understanding patterns of co-occurrence and biodiversity (Ricklefs, 2004).

Within the metacommunity framework, two complementary approaches have been used: one focuses on predictions of mechanistic models (Cottenie, 2005) and the other focuses on patterns of species distributions (Leibold & Mikkelsen, 2002). Although elucidating underlying mechanisms is an important aspect of ecological studies, it is often useful to identify patterns first in order to facilitate the detection of mechanisms. Metacommunity structures reflect multiple ecological processes that occur at multiple spatial scales and along a variety of environmental gradients (Leibold & Mikkelsen, 2002). A fundamental principle in ecology is that species richness along environmental gradients are Gaussian: modal in form with continuous distributions from one end of the spectrum to the other (Austin, 1985). That is, species should occupy a coherent range of sites along underlying environmental gradients.

For an entire metacommunity to exhibit coherence, the ranges of a majority of species must be moulded by the same environmental gradient (Presley *et al.*, 2010). However, the extent and location of species distributions along the gradient may differ. If species do not respond to the same environmental gradient, distributions will not form a coherent structure (Leibold & Mikkelsen, 2002). Strong competition may result in pairs of species with mutually exclusive ranges (Diamond, 1975). Checkerboard metacommunities are characterized by such mutually exclusive pairs of species that occur at random with respect to other such pairs or along different environmental gradients (Presley *et al.*, 2010). Nested structures occur when species-poor communities are subsets of species-rich communities (Patterson & Atmar, 1986). Nested distributions are characterized by less turnover in species composition along environmental gradients than expected by chance (i.e. negative turnover *sensu* Leibold & Mikkelsen, 2002), leading to predictable patterns of species loss associated with variation in species-specific characteristics (e.g. dispersal ability, habitat specialization, tolerance to

abiotic conditions). Examination of range boundaries within subsets can distinguish among three types of nested distributions: nested distributions with clumped, stochastic, or evenly spaced species loss (Presley *et al.*, 2010).

Conceptual models characterized by positive species turnover (i.e. more species turnover than expected by chance) can be distinguished by how range boundaries are distributed along environmental gradients (i.e. clumped, evenly dispersed, stochastic). Clumped boundaries indicate that species form compartments (groups of sites with similar species composition that are distinct from other such groups of sites; *sensu* Lewinsohn *et al.*, 2006), and are characteristic of Clementsian structures (Clements, 1916). Similar species distributions may result from shared evolutionary history and inter-dependent ecological relationships. Stochastic turnover is characteristic of Gleasonian structures, with species-specific responses resulting from chance similarities in environmental requirements or tolerances of species (Gleason, 1926). Finally, evenly spaced range boundaries are indicative of strong interspecific competition and trade-offs in competitive ability that manifest as distributions that are evenly spaced along environmental gradients (Tilman, 1982).

Deforestation and habitat fragmentation

Forests currently cover ~31% of the total land area, accounting for over 4 billion hectares of Earth's surface (FAO, 2010). The Atlantic Forest (AF) of South America is a complex rainforest system with an extensive range from tropical, coastal northeastern Brazil to subtropical, land-locked eastern Paraguay. The AF harbours highly diverse animal communities (Costa *et al.*, 2000) and is second only to the Amazon in number of endemic species associated with a South American biome (Costa *et al.*, 2000). Richness and distributional patterns of faunal groups in the AF are often defined spatially by vicariance events and historical locations of glacial refugia (Costa *et al.*, 2000; Carnaval *et al.*, 2009; Costa & Leite, 2012), resulting in centres of endemism comprised of many species that exhibit similar geographic distributions (Costa & Leite, 2012). The Interior AF is distinct from the Coastal AF, and has its own floristic (Oliveira-Filho & Fontes, 2000) and faunal characteristics (Chebez & Massoia, 1996). Variation in temperature and humidity associated with spatial variation in elevation and latitude contribute to differences between interior semi-deciduous AF and coastal evergreen AF (Oliveira-Filho & Fontes, 2000).

Like tropical forests throughout the world, AF has experienced wide-spread and intense deforestation, leaving only 9–16% of the original forest intact (Ribeiro *et al.*, 2009). Deforestation decreases the geographic extent of forests, divides larger forested areas into smaller fragments and increases isolation between fragments (Fahrig, 2003). Effects of deforestation can manifest at a broad range of spatial scales, including changes in microclimatic conditions (Didham & Lawton, 1999), species abundances and community composition (Ewers & Didham, 2005), geographic distributions of

species (Hames *et al.*, 2001; Ewers & Didham, 2005) and effects on global climate change (Travis, 2003). In terms of biological conservation, a comprehensive understanding of how species are spatially distributed within and among fragmented habitats (i.e. metacommunity structure), and how that structure changes through time is required to establish effective long-term conservation policy (Fischer & Lindenmayer, 2006).

Deforestation of the AF has resulted in a highly fragmented system in which isolated areas harbour communities that are connected via dispersal. This metacommunity is a useful model to evaluate how anthropogenically driven habitat fragmentation may alter historical species distributions. If current biogeographic patterns are influenced primarily by historical processes rather than by anthropogenically generated fragmentation, metacommunity structure should be Clementsian, with compartments consistent with natural areas of endemism (Costa *et al.*, 2000). In addition, the environmental gradients that define metacommunity structures should be associated with spatial variation in climate throughout the region. Alternatively, if habitat loss and fragmentation have dramatically changed the distributions of species, then non-Clementsian structures are expected or if Clementsian, compartments would not be consistent with historical areas of endemism. In addition, fragment size and isolation may be correlated with the gradients along which metacommunities are structured or stochastic extinction events may result in non-coherent structures.

Non-volant small mammals are useful for evaluating the effects of habitat fragmentation on populations, communities and metacommunities in the AF because they are abundant and taxonomically diverse, have small home ranges and vary greatly in their responses to environmental variation (Barret & Peles, 1999). Some small mammal species disperse between fragments and into the habitats surrounding fragments (Pires *et al.*, 2002; Pardini, 2004; Umetsu & Pardini, 2007; Umetsu *et al.*, 2008), whereas other species are sensitive to deforestation and cannot maintain positive population growth in non-forest habitats (Umetsu & Pardini, 2007; Umetsu *et al.*, 2008). In addition, small mammals represent groups that differ in ecology (e.g. diet, reproductive mode, dispersal ability) and evolutionary origin (e.g. marsupials of South American origin versus rodent invaders from North America; Voss & Jansa, 2003; Steppan *et al.*, 2004), which may result in taxon-specific responses to habitat loss and fragmentation.

To better understand the effects of fragmentation in the AF on the geographic distributions of small mammals, we address four inter-related questions: (1) Is metacommunity structure consistent with areas of endemism or has habitat loss and fragmentation altered patterns of species distribution? (2) Do patterns of metacommunity structure differ among evolutionary lineages (e.g. marsupials versus rodents) that differ in ecological function, diet, and dispersal ability? (3) Are species distributions moulded by spatially structured climatic factors, indicating that geographic distributions generally are constrained by non-anthropogenic environmental variation? (4) Is metacommunity structure associated with

forest fragment size, indicating that patch size and isolation has fundamentally changed species distributions?

METHODS

Data

We used information from 20 published studies (Appendix S1 in Supporting Information) that reported non-volant small mammal survey results from forest fragments distributed throughout the AF biome. Data represented samples from 76 fragments, with species richness ranging from 2 to 24. Identifications were assumed to be correct as presented in the original studies (Appendix S1). Species names were updated to current taxonomic nomenclature (Christoff *et al.*, 2000; Voss *et al.*, 2005; Weksler *et al.*, 2006; Weksler & Percequillo, 2011). Individuals not identified to species were omitted from analysis. Species reported from two or fewer sites were omitted from analysis because distributions of these species along spatial or environmental gradients in AF are poorly defined. In addition, species recorded from one site can bias analysis of boundary clumping because both range boundaries occur at the same site. Nonetheless, an evaluation of effects of such species showed that they have little impact on metacommunity structure, even when comprising 1/3 of all species (Presley & Willig, 2010).

Rodents comprise more than half of the mammal species in the Neotropics (Solari *et al.*, 2012), including at least 85 genera of the Sigmodontinae (Salazar-Bravo *et al.*, 2013). Sigmodontinae is the most species-rich group of mammals in the AF, despite only recently invading South America with estimated arrival approximately 4–12 MYA (Steppan *et al.*, 2004). Didelphid marsupials are the most diverse lineage of old endemic Tertiary non-volant small mammals of South American origin (Voss & Jansa, 2003). To determine whether response to fragmentation is specific to evolutionary lineages that differ greatly in their ecology, analyses were conducted for all small mammals combined and separately for marsupials, for all rodents, and for sigmodontine rodents only. Because of the distinction between Coastal AF and Interior AF, we conducted analyses separately for all sites combined and for only Coastal AF. Only five sites represented Interior AF, which is too few to conduct a powerful or meaningful evaluation of metacommunity structure.

Elements of metacommunity structure

Elements of metacommunity structure (EMS) analyses three aspects of species distributions (i.e. coherence, turnover, and boundary clumping) to determine which idealized pattern (Leibold & Mikkelsen, 2002) or quasi-structure (Presley *et al.*, 2010) best-fit empirical observations (Fig. 1). Data matrices were ordinated via reciprocal averaging, which arranges sites based on similarities in species composition and arranges species based on similarities in distribution (Gauch, 1982; Leibold & Mikkelsen, 2002). Coherence was

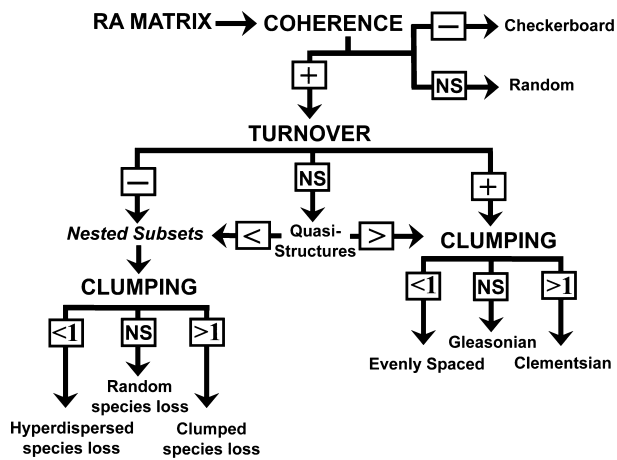


Figure 1 Flowchart showing the combinations of results for analyses of coherence, range turnover and range boundary clumping that are consistent with 14 types of metacommunity structure (Leibold & Mikkelsen, 2002; Presley *et al.*, 2010). Analyses are performed on a site by species matrix subjected to reciprocal averaging. Statistical results and significance are designated in boxes (modified from Presley *et al.*, 2010).

assessed statistically by counting the number of embedded absences in the ordinated matrix and comparing that value to a null distribution. If the number of embedded absences is not significantly different from expectations, a preponderance of species do not respond to the same environmental gradient and metacommunity structure is random. Significantly more embedded absences (i.e. negative coherence) than expected is indicative of checkerboards (Fig. 1). Significantly fewer embedded absences than expected is indicative of coherence and requires evaluation of range turnover and boundary clumping to distinguish among 12 possible coherent structures (Presley *et al.*, 2010).

Turnover was assessed by counting the number of replacements along the latent gradient and comparing the empirical value to a null distribution (Leibold & Mikkelsen, 2002). Fewer replacements than expected is consistent with nested distributions, whereas more replacements than expected require analysis of boundary clumping to differentiate among evenly spaced, Gleasonian or Clementsian distributions (Leibold & Mikkelsen, 2002). Analysis of boundary clumping can also distinguish among three types of nested structure (Presley *et al.*, 2010). Quasi-structures have turnover indistinguishable from that expected by chance, but have structures consistent with the conceptual underpinning of Clementsian, evenly spaced, Gleasonian or nested distributions (Presley *et al.*, 2010). Boundary clumping was quantified using Morisita's index and statistically evaluated via a χ^2 goodness-of-fit test that compared the observed distribution to an expected equiprobable distribution of range boundaries. Additional details about analyses of EMS are available elsewhere (Leibold & Mikkelsen, 2002; Presley *et al.*, 2009, 2010). All analyses of EMS were conducted with algorithms written in MATLAB 7.5 (script files available at <http://faculty.tarleton.edu/higgins/metacommunity-structure.html>).

Complementary analyses for EMS

Complementary analyses are required to better understand details of metacommunity structures as well as the environmental gradients represented by the primary axes along which the metacommunity is structured. We used the multiplicative model for partitioning diversity (Jost, 2006) in combination with hierarchical cluster analysis to determine the number and locations of compartments in Clementsian structures, respectively. This approach allows for unbiased determination of how many compartments are recognized and which sites belong to the same compartment. For each metacommunity, we used the multiplicative model ($\gamma = \alpha \times \beta$) of diversity partitioning to decompose γ -diversity into within-community (α) and among-community (β) components (Whittaker, 1960); α -diversity estimates the mean number of species per site, whereas β -diversity estimates the number of compositionally distinct communities that occur in a metacommunity (Jost, 2006). Cluster analysis was performed using an unweighted pair-group method with arithmetic means based on Sørensen (1948) distances estimated from presence/absence data. The number of basal clades equal to β was recognized as compartments.

We used canonical correspondence analysis (CCA) to determine which environmental variables were associated with gradients along which metacommunities were structured (Ter Braak, 1986). CCA is a marriage of reciprocal averaging and multiple regression. Consequently, CCA axes are defined by the same ordination used for EMS, resulting in a powerful method for determining associations of environmental factors with metacommunity structure. We used 19 climatic variables available via BioClim (Hijmans *et al.*, 2005; <http://www.worldclim.org/bioclim>), which were derived from monthly temperature and rainfall values from interpolated climate surfaces from global land areas. Fragment size was included as an additional environmental factor to determine whether it is associated with metacommunity structure. CCA was conducted in the R programming environment using the `cca` function from the 'vegan' package (R Core Team, 2012; Oksanen *et al.*, 2013).

Distance–decay relationships evaluate patterns of spatial autocorrelation and can be useful for understanding spatial structure in data (Morlon *et al.*, 2008). We created pairwise distance matrices of assemblage composition based on Sørensen distances and of geographic location based on Euclidean distances. We used a simulation with 1000 permutations to determine the significance of Pearson product-moment correlations between assemblage composition and geographic distances in the R package 'simba'. We used a simulation with 1000 permutations to determine the significance of Pearson product-moment correlations between assemblage composition and geographic distances in the R package 'simba'. We tested for differences in the slopes of distance–decay relationships for each possible pair of species groups using functions `diffslope` in package 'simba' (Jurasiński & Retzer, 2012). The `diffslope` function compares the empirical difference between

slopes to a null distribution of slope differences created by a permutation test to determine whether two slopes are significantly different. In addition, we created pairwise distance matrices based on climate and fragment size using Euclidean distances and used Mantel tests to evaluate the significance of correlations between assemblage composition and each of these environmental matrices for each species group.

RESULTS

In total, 87 species of non-volant small mammals were reported from 76 sites distributed throughout the AF (i.e. $\gamma = 87$). Of those, 41 species (47.1%) were found at more than two sites and were included in analyses of metacommunity structure; these species were comprised of 15 marsupials and 26 rodents with 22 (84.6%) belonging to the subfamily Sigmodontinae. The average number of species per site (i.e. α -diversity) was 7.1, with three marsupials (*Didelphis aurita*, 60.5% of sites; *Metachirus nudicaudatus*, 50.0%; and *Marmosa demerarae*, 39.5%) and three sigmodontines (*Nectomys squamipes*, 47.4%; *Akodon cursor*, 40.8%; and *Oligoryzomys nigripes*, 35.5%) occurring most frequently. The best-fit pattern of metacommunity structure was Clementsian (Table 1), with ranges of rodent species contributing the most to those patterns (Fig. 2). In contrast, marsupials exhibited Gleasonian structure. In general, estimates of β suggest that each Clementsian structure had six compartments, with β ranging from 5.8 (entire assemblage) to 6.5 (all rodents). In general, the same four biogeographic compart-

ments were observed regardless of species group, including (1) a compartment in the coastal Bahia State in Brazil, (2) a unique group in northeastern Brazil, (3) a south-eastern Brazil group, and (4) a compartment in the Interior AF (Figs 3 and 4).

Reciprocal averaging and CCA axes were highly correlated (Spearman $\rho = 0.96$, $P < 0.001$), indicating that axes from both analyses represent variation in the same latent environmental gradient. Variation in temperature was most highly associated with axes along which metacommunities were structured (Table 2). No environmental variable was highly associated (i.e. loading < -0.500 or > 0.500) with the primary axis for the marsupial metacommunity. Fragment size was only highly associated with the axis for the entire metacommunity. Temperature seasonality (BC4) and Isothermality (BC3) were the environmental factors most highly associated axes for the entire assemblage, rodents and sigmodontines, with other aspects of temperature being highly associated with the rodent or sigmodontine metacommunity (Table 2).

Significant distance–decay relationships existed for each species group (entire assemblage: $r = 0.455$, $P < 0.001$; marsupials: $r = 0.364$, $P < 0.001$; rodents: $r = 0.373$, $P < 0.001$; sigmodontines: $r = 0.358$, $P < 0.001$). Based on permutation tests, rodent (slope = -0.019) and sigmodontine (slope = -0.019) assemblage compositions changed significantly more quickly than did those of the entire assemblage (slope = -0.016) or marsupials (slope = -0.016). Matrix correlations showed that spatial variation in assemblage composition was highly associated with spatial variation in climate (entire assemblage: $r = 0.456$, $P < 0.001$; marsupials: $r = 0.345$,

Table 1 Results of analyses of coherence, species turnover and boundary clumping for small mammals from Atlantic Forests

Geographical extent Species group	Coherence			Species turnover			Boundary clumping		Metacommunity structure	β
	Abs	<i>P</i>	Mean	Rep	<i>P</i>	Mean	I	<i>P</i>		
Atlantic rain forest										
All species	1147	< 0.001	1702	155,087	< 0.001	84,623	1.65	0.001	Clementsian	5.780
75 sites, 41 species										
Marsupials	346	< 0.001	495	19,083	0.010	10,439	1.11	0.390	Gleasonian	4.205
74 sites, 15 species										
Rodents	543	< 0.001	819	43,425	0.002	27,129	1.92	0.001	Clementsian	6.500
67 sites, 26 species										
Sigmodontines	399	< 0.001	659	27,944	0.007	18,222	2.20	0.001	Clementsian	5.861
65 sites, 22 species										
Coastal										
All species	1139	0.011	1312	80,740	0.011	55,224	2.42	< 0.001	Clementsian	5.317
70 sites, 36 species										
Marsupials	317	0.004	406	12,390	< 0.001	4449	2.68	0.001	Clementsian	3.864
69 sites, 14 species										
Rodents	398	< 0.001	631	34,443	0.939	34,033	2.59	< 0.001	Quasi-Clementsian	5.636
64 sites, 20 species										
Sigmodontines	249	< 0.001	431	17,271	0.004	10,444	2.76	< 0.001	Clementsian	5.050
60 sites, 17 species										

Analyses were performed for all species and for each of three taxonomically defined subgroups.

Significant results ($P \leq 0.05$) are bold.

Abs, number of absences; Rep, number of replacements; I, Morisita's index; β , beta diversity (i.e. estimated number of compartments).

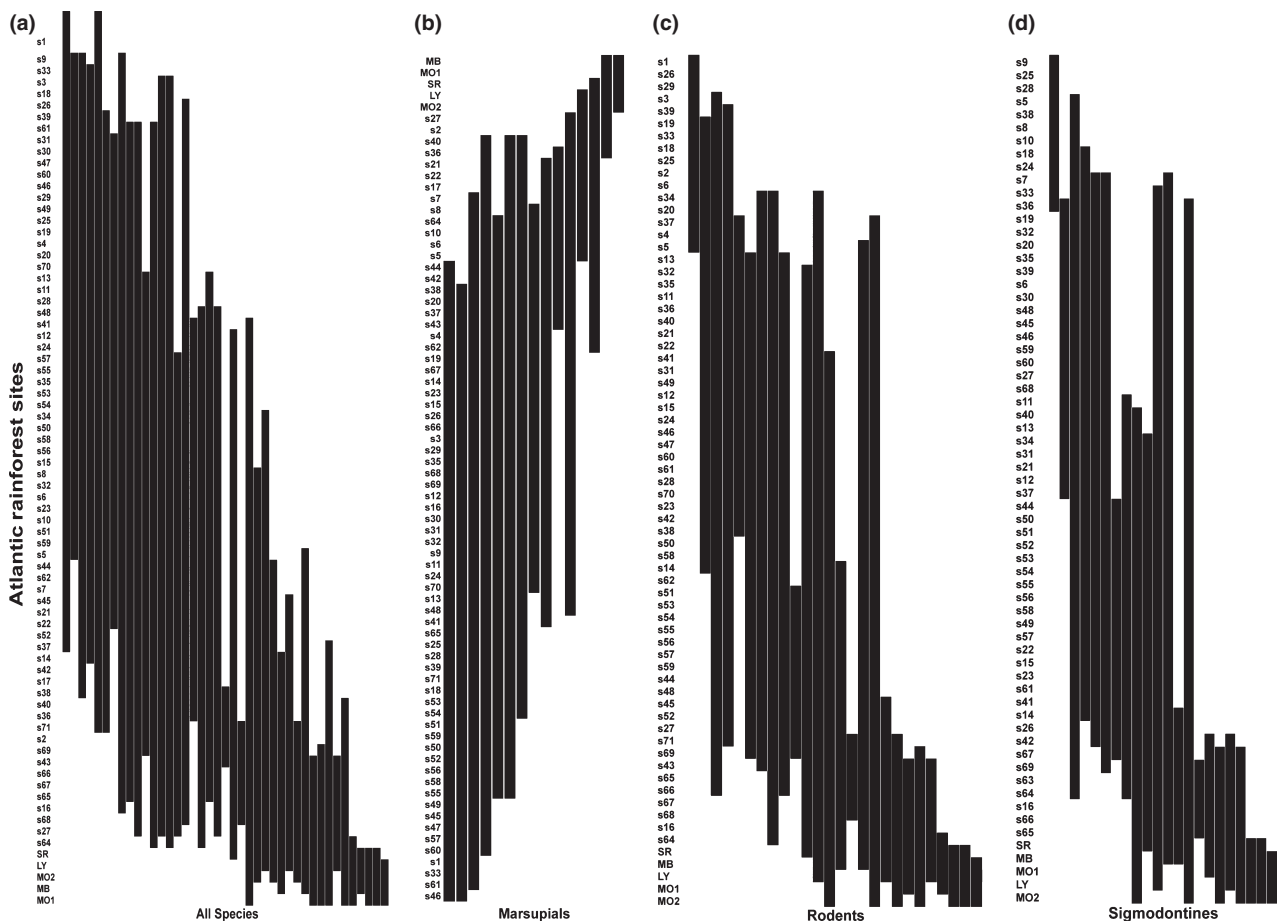


Figure 2 Species distributions (vertical black bars) of each assemblage evaluated a) all species, b) marsupials, c) rodents, and d) sigmodontine rodents, along latent environmental gradients with sites and species ordered according to the primary axis extracted via reciprocal averaging. Because each structure exhibited coherence, embedded absences were filled to visualize the pattern of turnover and range boundary clumping.

$P < 0.001$; rodents: $r = 0.452$, $P < 0.001$; sigmodontines: $r = 0.448$, $P < 0.001$), as well as with spatial variation in fragment size (entire assemblage: $r = 0.164$, $P = 0.010$; marsupials: $r = 0.160$, $P = 0.023$; rodents: $r = 0.153$, $P = 0.013$; sigmodontines: $r = 0.158$, $P = 0.008$).

DISCUSSION

Three proposed mechanisms could contribute to species distributions and emergent metacommunity structures of non-volant small mammals in the AF: (1) habitat use based on refugia from the expansion and contraction of glaciers during the Pleistocene (Carnaval & Moritz, 2008), (2) vicariance events associated with large rivers that defined boundaries of some areas of endemism (Costa & Leite, 2012), and (3) altered spatial distributions driven largely by habitat loss and fragmentation (Turner, 1996; Laurance *et al.*, 2002). Because fragmentation from anthropogenic activities has been extensive and pervasive in the AF, it has the potential to affect the distributions of species throughout the biome, causing differences between extant patterns and those expected based on historical biogeography. However, our

results showed that the Clementsian structure of small mammal metacommunities in the AF was more consistent with expectations based on a combination of glacial refugia and vicariance events than if habitat fragmentation was the primary driver. Habitat loss and fragmentation from anthropogenic activities have not changed distributions enough to mask historical signals. Nonetheless, extinction debt may exist as populations in smaller fragments may be exposed to increased stochastic extinction events, with isolation of fragments reducing the likelihood that rescue effects can sustain such populations (Kuussaari *et al.*, 2009; Metzger *et al.*, 2009).

Metacommunity structure in the Atlantic Forest

The AF exhibits a great deal of geographic variation in biotic and abiotic characteristics, with multiple areas of endemism (Costa *et al.*, 2000; Costa & Leite, 2012). Although marsupials had Gleasonian structure, the remaining evolutionary lineages and the entire assemblage were Clementsian with multiple compartment locations consistent with identified areas of endemism (Fig. 4). The compartmentalized structure we observed supports previous studies by identifying distinct

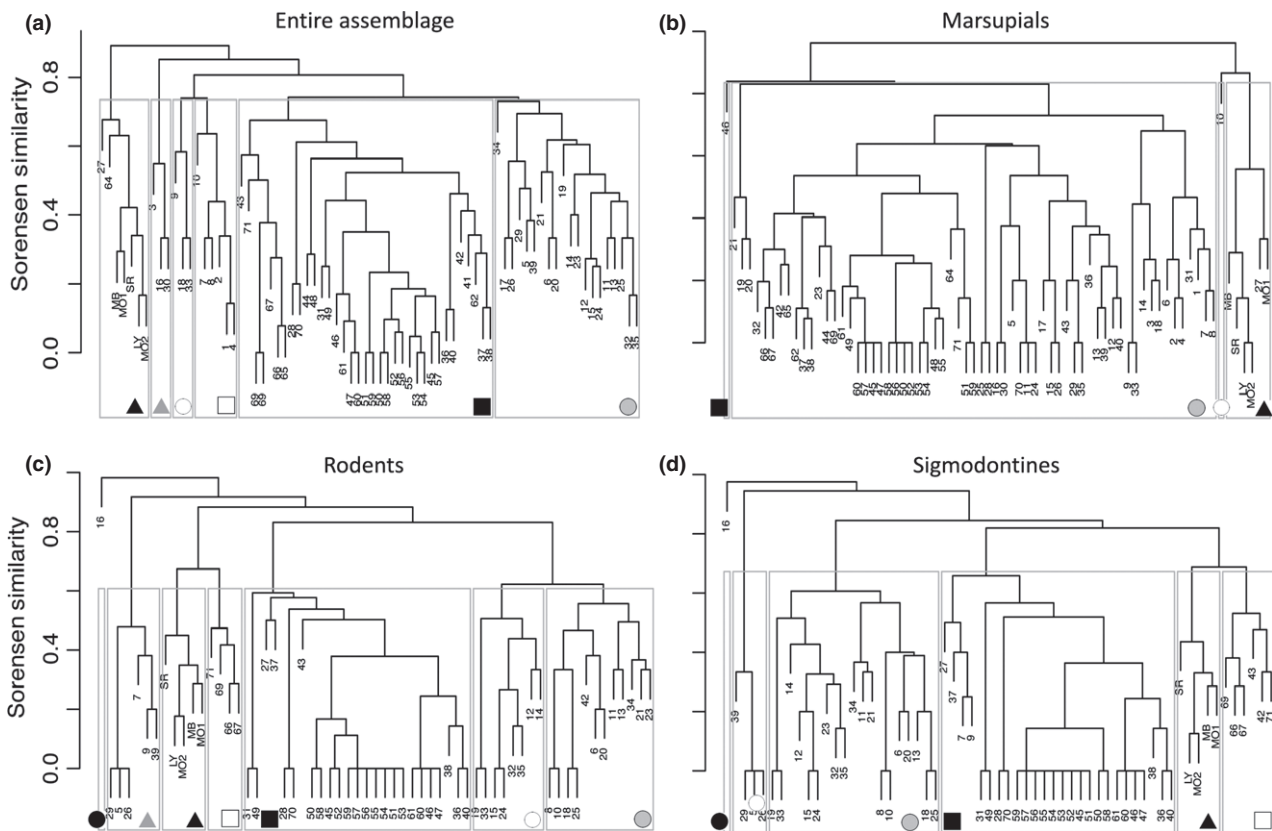


Figure 3 Dendrograms showing relationships of sites based on presence/absence data using unweighted pair-group method with arithmetic means based on Sørensen (1948) distances for (a) the entire small mammal assemblage, (b) marsupials, (c) rodents, and (d) sigmodontine rodents. Gray boxes indicate distinct faunal compartments for each metacommunity equal to multiplicative β . For the entire assemblage, rodents and sigmodontine rodents, shading represents distinct compartments associated with Clementsian structures (i.e. the number of basal clades equal to β). Marsupials had Gleasonian structure, which do not form compartments. Site codes are in Appendix S1.

species clusters corresponding to different biogeographic regions. These regions coincided largely with major river basins, such as the area between Rio São Francisco and Rio Doce (Carnaval *et al.*, 2009), the area between Rio Doce and Rio Jequitinhonha (Costa & Leite, 2012), and the proposed Bahia refugium (Carnaval *et al.*, 2009). For rodents and sigmodontines, additional compartments mirrored the Paulista centre of endemism (Costa *et al.*, 2000). The fact that species clusters corresponded to areas of endemism suggests that forest fragmentation has had little effect on the metacommunity structure of non-volant, small mammals in the AF. Forest fragmentation is documented to affect the geographic distribution of species (Turner, 1996; Laurance *et al.*, 2002; Costa & Leite, 2012); however, this is the first study to evaluate such effects on emergent metacommunity structures. A study of temporal changes in metacommunity structure of an English woodland found no change in structure despite changes in the distributions of species and community composition over that time period (Keith *et al.*, 2011). In conjunction, these studies suggest that metacommunity structure in some systems may be relatively stable through time even when exposed to anthropogenic activities and changes in the distributions of some species and the compositions of local communities.

Synthesis of phylogeographic studies of birds, frogs and mammals from AF suggest that rivers delineate the geographic boundaries for many species (Costa & Leite, 2012). A phylogeographic break occurs near the Rio Doce and is suggestive of a vicariant event that has affected many vertebrate orders. For the entire small mammal assemblage, the Rio Doce is the southernmost boundary for compartment AFAll1, which extends from northeastern Brazil. In addition, compartment AFAll4 is restricted to areas south of the Rio Doce (Fig. 3a), and the Rio Jequitinhonha is the northernmost boundary for several compartments. Similar to the case for all small mammals, rodent and sigmodontine metacommunities formed a northeastern Brazil compartment with the Rio Doce as its southern limit. In contrast, compartments in the coastal marsupial metacommunity were not defined by the locations of rivers. A metacommunity approach is a powerful approach to detect effects of vicariance events because it simultaneously evaluates responses of an entire assemblage.

The entire non-volant small mammal fauna of Paraguay consistently formed a distinct compartment along with other Interior AF sites. Paraguayan AF fragments have non-volant small mammal communities comprised of species that phylogenetically are closely related to species from three different

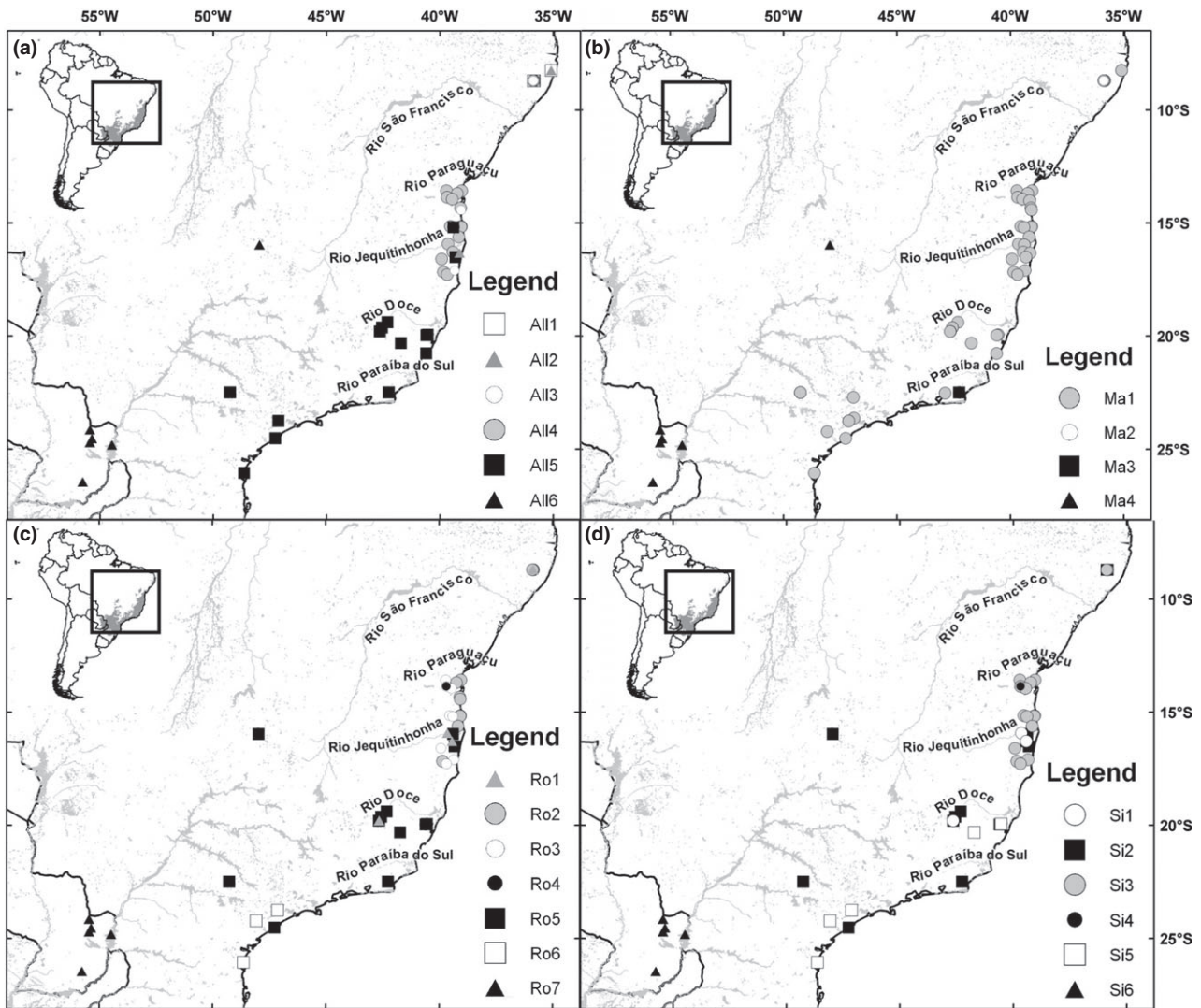


Figure 4 Maps showing sites that represent distinct compartments for (a) the entire assemblage, (b) marsupials, (c) rodents and (d) sigmodontine rodents. For the entire assemblage, rodents and sigmodontine rodents, symbols represent distinct compartments associated with Clementsian structure. Marsupials had Gleasonian structure, which is not characterized by clumped species boundaries that delineate compartments. The number of recognized faunal groups for each metacommunity was determined by multiplicative β , and group membership was determined by cluster analysis (Fig. 3). Symbols for sites are the same as those in Fig. 3.

regions (de la Sancha, 2014): (1) southern coastal AF, including parts of Argentina, Uruguay and south-eastern Brazil (de la Sancha *et al.*, 2009, 2012; Valdez & D'Elía, 2013), (2) central and northern Brazil (de la Sancha *et al.*, 2011), and (3) the Chaco and Cerrado of Paraguay and Brazil (de la Sancha, 2014). The presence of Paraguayan compartments supports the contention that coastal and interior portions of the AF are distinct biogeographical units (Chebez & Massoia, 1996).

Forest fragmentation at a biogeographical scale

Fragmentation throughout the AF has been studied extensively (Pardini & Umetsu, 2006; Ribeiro *et al.*, 2009; de la Sancha, 2014); however, the history of deforestation in this region is difficult to document prior to the 1970s when satellite images became available (Ribeiro *et al.*, 2009). In

addition, few studies on the effects of deforestation on small mammal distributions predate 2000 (Appendix S1). Recent studies are improving the understanding of species distributions for small mammals in the AF (Pardini & Umetsu, 2006; de la Sancha, 2014); however, reliable data for small mammal distributions prior to extensive habitat loss and fragmentation in AF are lacking, and major gaps in fundamental understanding remain, particularly in the interior AF of Paraguay and Argentina. The greatest documented richness of mammals in the AF occurs between São Paulo and Rio de Janeiro (Costa *et al.*, 2000). Despite using species richness from individual forest fragments and not cumulative species lists from distribution maps, our results are consistent with this pattern of richness, suggesting that the data used (Appendix S1) were sufficient to reflect biogeographic patterns in AF.

Table 2 Loadings of the first axis from canonical correspondence analysis (CCA) for all non-volant small mammals and separately for each taxonomic subgroup based on area of forest remnants and nineteen BioClim variables (Hijmans *et al.*, 2005).

Codes	Bioclimatic variables	All	Marsupials	Rodents	Sigmodontines
	Eigenvalue	0.604	0.624	0.638	0.633
	% Inertia	0.141	0.194	0.141	0.153
Area	Area of Remnants	-0.528	-0.429	-0.492	-0.494
BIO1	Annual Mean Temperature	0.212	-0.053	0.408	0.382
BIO2	Annual Mean Temperature	-0.394	-0.203	-0.525	-0.481
BIO3	Isothermality	0.609	0.284	0.710	0.734
BIO4	Temperature Seasonality	-0.745	-0.437	-0.853	-0.850
BIO5	Max Temperature of Warmest Month	-0.384	-0.418	-0.299	-0.285
BIO6	Min Temperature of Coldest Month	0.453	0.141	0.657	0.628
BIO8	Mean Temperature of Wettest Quarter	-0.009	-0.065	0.102	0.072
BIO9	Mean Temperature of Driest Quarter	0.427	0.086	0.637	0.621
BIO10	Mean Temperature of Warmest Quarter	-0.154	-0.271	-0.021	-0.047
BIO11	Mean Temperature of Coldest Quarter	0.434	0.102	0.649	0.626
BIO12	Annual Precipitation	-0.342	-0.189	-0.383	-0.408
BIO13	Precipitation of Wettest Month	-0.074	0.029	-0.182	-0.181
BIO14	Precipitation of Driest Month	-0.362	-0.258	-0.323	-0.352
BIO15	Precipitation Seasonality (Coefficient of Variation)	0.31	0.232	0.251	0.275
BIO16	Precipitation of Wettest Quarter	0.022	0.094	-0.073	-0.077
BIO17	Precipitation of Driest Quarter	-0.332	-0.233	-0.295	-0.322
BIO18	Precipitation of Warmest Quarter	-0.052	0.188	-0.195	-0.211
BIO19	Precipitation of Coldest Quarter	-0.021	-0.119	0.019	-0.001

Correlations greater in magnitude than 0.500 are bold.

Atlantic Forest is a dynamic system with about 50% of the land area changing cover type every 20 years, with natural regeneration of forests offsetting much of modern deforestation (Metzger *et al.*, 2009). In addition, forest fragments change in size and connectivity to other forest patches through time. In highly dynamic conditions such as those in the AF, landscape configuration is not expected to exhibit a large effect on the richness or distribution of organisms (Fahrig, 2005). The failure of forest loss and fragmentation to demonstrably alter the metacommunity structure of small mammals is consistent with this expectation.

The relatively recent and ongoing nature of fragmentation in the AF suggests that extinction debt may be due for AF fragments (Hanski & Ovskainen, 2002). However, analysis of the effects of past and present landscape structure on small mammal richness in southern coastal AF suggested that extinction debt has mostly been paid already for this group (Metzger *et al.*, 2009). By comparison, larger extinction debts existed for plants, frogs and birds. Small mammals that are forest specialists appear to go locally extinct relatively quickly in fragmented AF, whereas populations of non-specialists persist as species are able to use matrix habitats to disperse between forest patches, allowing rescue effects to reduce effects of extinction debt (Metzger *et al.*, 2009). Short extinction time-lags for forest specialists may explain why a large proportion (53%) of species was recorded from only one or two of the 75 fragments. It is likely that many of these metapopulations of forest specialists will eventually go extinct if current forest cover and

connectivity are maintained in the long term (Hanski & Ovskainen, 2002).

Environmental gradients

The environmental factors most associated with metacommunity structures of non-volant small mammals were temperature seasonality (BC4) and isothermality (BC3), each of which reflects the equality of temperature through time, suggesting that spatial variation in the environment was a more important driver of metacommunity structure than fragment size. Nonetheless, area of fragments was among the three most associated environmental factors for the non-volant small mammal metacommunity and for the marsupial metacommunity. In general, environmental variation is spatially structured, which typically results in spatially structured variation in assemblage composition (i.e. distance-decay relationships). Variation in climate explained about three times more of the variation in assemblage composition among sites than did variation in fragment size (see Results of Mantel tests). This suggests that spatial variation in the environment remains of primary importance in determining the composition of communities. Importantly, mammals typically respond indirectly to variation in climate and directly to variation in biotic (e.g. vegetation, resource abundance) aspects of the environment (Andrews & O'Brien, 2000; Ernest *et al.*, 2000). We used climatic factors because they were the only environmental data available for all sites; however, if suitable biotic environmental data

(e.g. vegetational composition or complexity) were available it is likely that spatial variation in the environment would explain a greater portion of spatial variation in small mammal composition. Despite extensive habitat degradation, loss and fragmentation throughout AF, small mammal assemblages harboured by current forest fragments maintain expected biogeographical patterns associated with historical refugia, vicariance events and spatial variation in climate. This suggests that species distributions, community composition and metacommunity structure may be somewhat robust with respect to intense and pervasive anthropogenic disturbance.

Final summary

Atlantic Forest rodents exhibited Clementsian structure defined by multiple distinct compartments along a gradient associated with variation in temperature seasonality. These compartments (Figs 3 and 4) were spatially consistent with centres of endemism and historic refugia (Costa *et al.*, 2000; Carnaval & Moritz, 2008). In addition, boundaries of compartments are closely associated with large rivers, which are important barriers associated with vicariance events in AF (Costa & Leite, 2012). In contrast, marsupials had Gleasonian metacommunity structure, indicating that metacommunity structure and the relative importance of vicariance events to the formation of compartments may depend on the ecology or evolutionary history of the taxonomic group.

Despite extensive habitat loss and fragmentation, small mammals in AF have maintained their expected biogeographical affinities, as delineated compartments are consistent with proposed centres of endemism, refugia and vicariance events. However, the continued high rate of habitat loss and increasing fragmentation indicates that extinction debt may exist. While it has been suggested that small mammals in the AF show weak responses to past landscape structure and dynamics (Metzger *et al.*, 2009), extinction debt may confound attempts to associate pattern to process, especially for species such as non-volant small mammals that can maintain viable populations in relatively small forest fragments. These results suggest that any effective conservation plan in AF must: 1) consider each area of endemism to maintain regional biodiversity; and 2) maintain sufficiently large and connected forest fragments to prevent high extinction debt associated with source-sink dynamics, isolation of fragments, decreased effective dispersal between fragments and stochastic extinction of small populations.

ACKNOWLEDGEMENTS

We thank John M. Bates, Shayna Harris and Nancy McIntyre for valuable comments on earlier drafts, field crews in Paraguay (Pastor E. Pérez, María Luisa Ortiz, Lourdes Valdez, and Julio Torres), the staffs at La Fundación Moisés Bertoni,

Guyra Paraguay, Reserva Morombí and Itaipú Binacional for logistical support and for access and stay at each of the Paraguayan reserves. Nancy McIntyre Texas Tech University (TTU) and Richard A. Nisbett (Department of Kinesiology, Rice University) helped with traps. Financial support for NdS was partially provided by a Fulbright Fellowship (Institute of International Education - US Department of State), The Marshall Field Collection Fund of Field Museum of Natural History, the Mary Rice Foundation, the American Philosophical Society through the Lewis and Clark Exploration Fund, a Latin American Award (American Society of Mammalogists), research assistantships from the Department of Biological Sciences, (TTU), a TTU Association of Biologists Mini-grant (TTUAB), the J. Knox Jones, Jr., Memorial Endowed Scholarship (TTU), the Michelle C. Knapp Memorial Scholarship (TTU), a AT&T McNair Fellowship, and a Hispanic Scholarship Fund Award. Curator assistance with specimens by Bruce Patterson, Bill Stanley and John Phelps (FMNH) and Robert J. Baker and Heath Garner (TTU) is greatly appreciated. S. Presley was supported by the Center for Environmental Sciences and Engineering at the University of Connecticut and by a Grant (DEB-0620910) from NSF to the Institute of Tropical Ecosystem Studies, University of Puerto Rico, and the International Institute of Tropical Forestry as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Locations, collection effort, and references for Atlantic Forest fragment data.

BIOSKETCH

Noé U. de la Sancha is an Assistant Professor at Chicago State University and a Research Associate at The Field Museum of Natural History. This study is derived from a

chapter of his dissertation. N.d.S. is interested in questions of biodiversity patterns that are driven by anthropogenic habitat changes.

Author contributions: N.d.S. originally conceived the idea and S.J.P., C.L.H. and R.E.S. considerably improved on it; N.d.S. collected the data; N.d.S., S.J.P. and C.L.H. analysed the data; C.L.H. developed the Matlab functions utilized. N.d.S. led the writing with considerable and substantial help from S.J.P. and C.L.H.

Editor: Karen Beard