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Seasonality in metacommunity structure: an empirical test in the Atlantic Forest

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Abstract

Context The metacommunity concept helps to understand how local and regional processes regulate species distributions in landscapes. Metacommunity structure is often assumed as static, but may be rather dynamic, following temporal changes along environmental gradients.

Objectives We present an empirical test of the temporal dynamics of metacommunity structure, using small mammals in an Atlantic Forest landscape as a model system.

Methods We analyzed incidence matrices using the Elements of Metacommunity Structure framework and evaluated whether local, landscape, and spatial factors structured the metacommunity during different climatic seasons (HS = humid; SHS = super-humid) and time periods (1 = 1999–2001; 2 = 2005–2009). We compared HS-1 and SHS-1 to evaluate if metacommunity structure varies between seasons, and HS-1 and HS-2 to evaluate if it varies between time periods.

Results Metacommunity structure changed from Clementsian (HS-1) to random (SHS-1), but during HS-2 it was Clementsian again. This suggests that groups of species are responding similarly to the major gradient of variation during the HS only. Patch size structured the metacommunity during both humid periods, and local habitat structure only during HS-1. We suggest that during the SHS these gradients are lost due to increased matrix permeability to movement, which homogenizes local communities resulting in a random structure.

Conclusions Species habitat requirements and specializations determined metacommunity structure, but only during the HS. The Clementsian structure indicates that forest disturbances may result in the loss of whole groups of species during the HS. Alternating patterns of metacommunity structure may be associated to changes on matrix suitability between seasons.

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Introduction

Community ecology traditionally explores local patterns of interactions between species and their abiotic environment to predict species abundances and distributions (Vellend 2010). However, the importance of regional processes to understand co-occurrence patterns of species has been increasingly acknowledged (Ricklefs 1987; Vellend 2010). In this sense, the metacommunity concept, defined as a set of local communities potentially linked by dispersal of interacting species, provides a useful unifying framework (Leibold and Mikkelson 2002; Leibold et al. 2004). This framework helps to understand how interactions between local (e.g., species interactions) and regional (e.g., dispersal) processes regulate species distributions in landscapes (Leibold and Mikkelson 2002; Leibold et al. 2004).

One key advantage of the metacommunity framework is the possibility to distinguish among several patterns of species distribution along environmental gradients that have historically been recognized by ecologists. Such distribution patterns include the Clementsian (Clements 1916), Gleasonian (Gleason 1926), checkerboard (Diamond 1975), evenly-spaced (Tilman 1982), and nested patterns (Patterson and Atmar 1986). To help identify the most likely pattern for a given metacommunity, Leibold and Mikkelson (2002) proposed the elements of metacommunity structure (EMS) framework, which is based on three statistics (coherence, turnover, and boundary clumping). By assessing the significance of these statistics and their values, it is possible to determine which metacommunity structure best describes the major pattern of species distribution (Leibold and Mikkelson 2002; Presley et al. 2010). For example, Gleasonian and Clementsian structures differ regarding whether species respond independently or similarly to the major gradient of variation, respectively (Clements 1916; Gleason 1926; Leibold and Mikkelson 2002).

Metacommunity structure is often treated as static, i.e. stable in time, thus assuming that only a single pattern or structure would describe a given

metacommunity during all time periods (e.g., Hylander et al. 2005; Presley et al. 2009). However, metacommunity structure may be rather dynamic, if local communities are affected by temporal changes that occur along environmental gradients (Datry et al. 2016; Sarremejane et al. 2017). Such dynamism may be driven by several factors, such as environmental disturbances (e.g., Bloch et al. 2007), long-term climate change (e.g., Gilman et al. 2010), and intra-annual climatic seasonality (e.g., Fernandes et al. 2014). These factors may cause changes in the abiotic environment, resource availability, population densities, and species interactions (Bloch et al. 2007; Gilman et al. 2010). These changes, by their turn, may favor some species while disfavoring others, ultimately increasing turnover or nestedness in species composition, potentially changing the dominant pattern of metacommunity structure. For instance, Bloch et al. (2007) documented temporal variability in the nestedness of terrestrial gastropods from Puerto Rico, the metacommunity being less nested immediately following a hurricane and becoming more nested during subsequent years.

Climatic seasonality, i.e. intra-annual variation in abiotic factors, is a potentially important factor driving temporal variation in metacommunity structure (e.g., Fernandes et al. 2014). Climatic seasonality may cause variation in the availability of food resources (Develey and Peres 2000; Naxara et al. 2009), habitat heterogeneity and complexity (Wojciechowski et al. 2017), and habitat stability (e.g., frequency of disturbances; Altermatt et al. 2009). Recent studies have evaluated the role of seasonality in structuring metacommunities at different spatial scales and for different taxa, including bats (e.g., Cisneros et al. 2015), small mammals (e.g., de la Sancha et al. 2014), arthropods (e.g., Altermatt et al. 2009; Sarremejane et al. 2017), and phytoplankton (e.g., Wojciechowski et al. 2017). Cisneros et al. (2015), for example, found season-specific and guild-specific distributional patterns for a bat metacommunity in a fragmented landscape, driven by an interaction between landscape characteristics and seasonal variation in resources. The gleaning animalivore group exhibited checkerboard and random structures during the dry and wet seasons, respectively (Cisneros et al. 2015). This change in metacommunity structure was explained by differences in resource availability between seasons and associated changes in the use of landscape by species

(Cisneros et al. 2015). The effects of seasonality on metacommunity parameters have also being demonstrated using other frameworks different from EMS. For example, climatic seasonality was associated with temporal variation in nestedness and turnover components of beta diversity of phytoplankton across subtropical reservoirs (Wojciechowski et al. 2017). Ruhí et al. (2017) also demonstrated seasonal variation on richness and replacement components of beta diversity in metacommunities of benthic invertebrates in intermittent rivers.

Seasonality can also change the relative importance of local (e.g., habitat structure) and landscape (e.g., patch size and isolation) factors on colonization-extinction dynamics in fragmented landscapes. For example, seasonality can mitigate or accentuate edge effects and disturbances on habitat structure inside small forest fragments (Machado and Oliveira-Filho 2010; Tscharntke et al. 2012). The effects of patch isolation can also vary seasonally, if dispersal rates among forest fragments vary between seasons, as detected for some mammals (Pires et al. 2002) and birds (Silva et al. 1996). In addition, matrix suitability may vary seasonally in many agricultural landscapes, as the planting and harvesting periods are often coupled with seasonal changes (e.g., Uzêda et al. 2011). Many studies have shown that matrix suitability regulates the movement of individuals across landscapes (e.g. Vandermeer and Carvajal 2001; Haynes and Cronin 2006), thus affecting species occurrence and abundance (e.g. Umetsu et al. 2008) and community structure within local habitat patches (e.g. review in Prevedello and Vieira 2010; Brady et al. 2011). Yet, it is still unclear whether temporal variations in matrix suitability affect overall metacommunity structure in agricultural landscapes. More generally, despite these previous studies, the interaction of climatic seasonality with local and landscape factors and their effects on species occurrences remain understudied.

Here we present an empirical test of the importance of temporal, local and landscape factors on metacommunity structure in fragmented landscapes. More specifically, we tested how metacommunity structure is affected by climatic seasonality, and if the pattern detected for a season (humid season) is consistently maintained during different time periods. For these purposes, we performed two complementary analyses for a small-mammal metacommunity in a fragmented landscape of the Atlantic Forest biodiversity hotspot, using a comprehensive empirical dataset spanning 10 years. In the first analysis, we tested for changes in metacommunity structure between climatic seasons (humid versus super-humid), comparing the EMS between seasons. In the second analysis, we tested for consistency in metacommunity structure between time periods (1999–2001 vs. 2005–2009). We also identified the environmental gradients structuring the metacommunity during each season and time period.

Materials and methods

Study area

The Macacu River river basin is located within the Brazilian Atlantic Forest and is dominated by forest fragments smaller than 160 ha (Vieira et al. 2009; Delciellos et al. 2016). These forest fragments are surrounded by a heterogeneous matrix composed mostly of pastures and plantations (Vieira et al. 2009; Delciellos et al. 2016). A total of 22 forest sites were sampled at the base of Serra dos Órgãos mountain range, in the municipalities of Guapimirim (22°20′S and 42°59′W), Cachoeiras de Macacu (22°28′S and 42°39′W), and Itaboraí (22°44′S and 42°51′W), state of Rio de Janeiro, Brazil (Fig. 1; Online Resource 1—ESM 1). Twenty sites were located in forest fragments, and two sites in continuous forest in the surroundings of the Serra dos Órgãos National Park. Samplings extended over an area of 189 km^2 (Fig. 1).

The vegetation of all 22 sites is dense evergreen forest (IBGE 2012). Vegetation of forest fragments is characterized by a canopy ca. 20 m high, with a higher presence of palms (e.g., *Astrocaryum aculeatissimum*), *Cecropia* spp., and lianas (Finotti et al. 2012; Delciellos et al. 2016) than in continuous forest sites. These species are frequently used as indicators of secondary forest succession (e.g., Oliveira-Filho et al. 2004; Castello et al. 2017). The vegetation of the two continuous forest sites is less disturbed than the vegetation in forest fragments (Freitas et al. 2005).

The climate in the study region is mild humid-mesothermic (Nimer 1989). The average annual rainfall is 1553.5 mm and the average annual temperature is 21.4 °C (data available at https://www.climatempo.com.br/). From October to March the
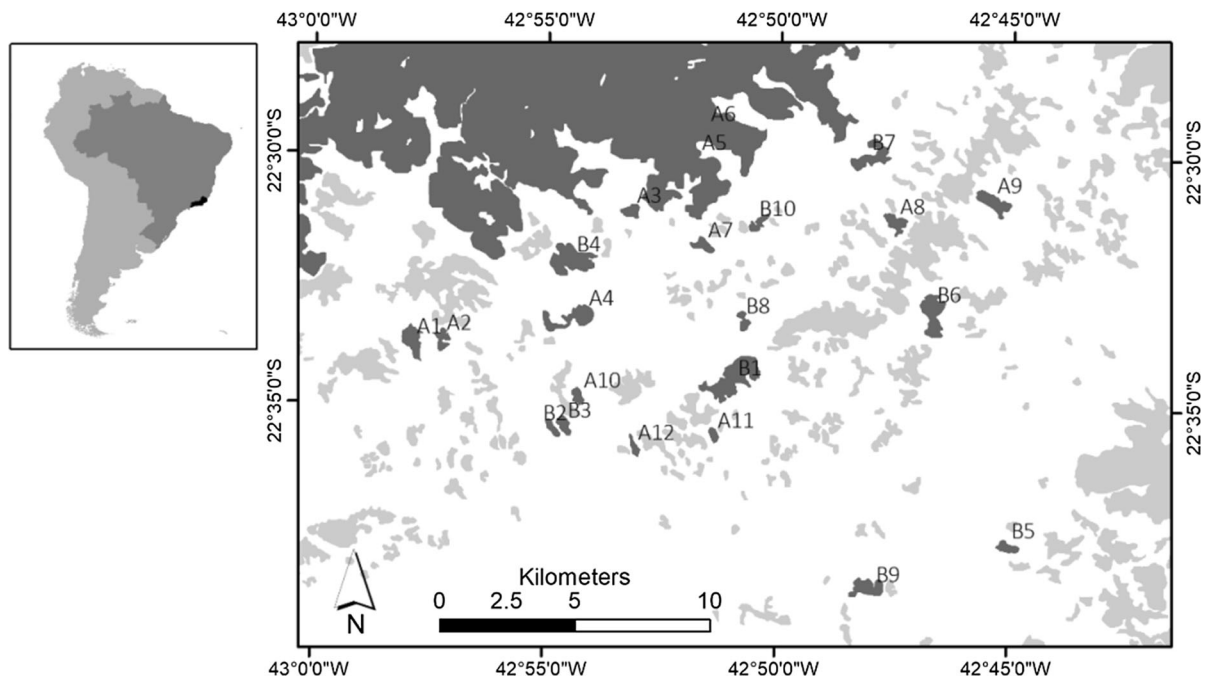
Fig. 1 Forest sites (N = 22) sampled in the Macacu River basin, Brazil. A1–A12: 12 sites sampled once from 1999 to 2001 during the super-humid and humid seasons; B1–B10: 10 sites sampled once from 2005 to 2009 during the humid season only

climate is super-humid (super-humid season; hereafter SHS), with average rainfall of 175.0 ± 55.8 mm, and from April to September the climate is humid (humid season; hereafter HS), with average rainfall 65.0 ± 19.8 mm (https://www.climatempo.com.br/). There are no months that are water deficit (https://www.climatempo.com.br/). In tropical forests productivity and fruit production are influenced by the variation in rainfall and length of the HS (Davis 1945; Morellato et al. 2000). Arthropod availability is frequently correlated with variation in rainfall, temperature and productivity; all of which are higher in the SHS (e.g., Naxara et al. 2009). Fruit production is also frequently higher in the SHS (e.g., Develey and Peres 2000). Both fruits and arthropods are the major food items of most non-volant small mammal species occurring in tropical forests (e.g., Naxara et al. 2009). Consequently, population dynamics of many of these species is coupled with seasonality (e.g., Gentile et al. 2004; Ferreira et al. 2016), potentially affecting metacommunity structure.

Field methods

From 1999 to 2001, 10 forest fragments (A1–A4, A7–A12) and two continuous forest sites (A5, A6) were sampled once during the humid (HS-1) and once during the super-humid (SHS-1) seasons, with approximately four to six months interval between samples at the same site (Fig. 1; Online Resource 1—ESM 1). Ten other forest fragments (B1–B10) in the same landscape were sampled once during the humid season (HS-2) between 2005 and 2009 (Fig. 1; Online Resource 1—ESM 1).

In each sampling session a standardized effort of 800 trap-nights was used to capture small mammals, belonging to the orders Rodentia and Didelphimorphia. Four transects were established from the matrix to the center of forest fragments, each transect with four trap stations placed 10 m apart in the matrix, one trap station on the forest edge, and 15 trap stations 20 m apart inside the forest fragment. Each trap station had two live traps on the ground, one Tomahawk® and one Sherman®. In six of these trap stations one of the live traps was set 1–2 m above the ground in tree branches, rather than on the ground. Transects were sampled for five consecutive nights. Captures in

the matrix were rare and had a negligible effect on the species composition of forest fragments, as most species captured in the matrix were also captured inside forest fragments. The exceptions were two invasive species (*Mus musculus* and *Rattus rattus*), which were not included in the analysis, and the rodent *Euryzygomatomys spinosus*, which was captured near the forest edge and also inhabits forests (Catzeflis et al. 2016). In the two continuous forest sites, methods and effort were the same as in the forest fragments, except that each transect was entirely within the forest, with the 20 trap stations 20 m apart. For further details, see Vieira et al. (2009) and Delciellos et al. (2016). Trapping and handling conformed to guidelines sanctioned by the American Society of Mammalogists (Sikes 2016).

Landscape variables

Four variables were measured to identify the environmental gradients related to landscape structure that may structure the metacommunity: (i) habitat amount, (ii) patch size, (iii) patch isolation, and (iv) distance to nearest continuous forest. The percentage of forest cover was used as a proxy of habitat amount, measured within a 900 m radius buffer surrounding the central coordinates of each site. The size of the buffer area (900 m radius) was chosen based on average maximum inter-fragment movement distances reported for didelphids in Atlantic Forest landscapes (Pires et al. 2002; Prevedello and Vieira 2010). Patch isolation was measured as the mean distance (in meters) between the focal (sampled) forest fragment and all other forest fragments present within a 900 m radius buffer (as in Crouzeilles et al. 2014; Delciellos et al. 2016). When no neighboring habitat patches were within the search buffer, we used the radius of the buffer (900 m) as the value of isolation. The landscape variables were obtained from the map produced by SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais (2005). Data were converted to UTM projection to assure accurate area and distance calculations. Habitat amount and patch isolation were measured using the software ArcGis 9.3 (ESRI 2008). The distance to nearest continuous forest, Serra dos Órgãos mountain range, was measured as the Euclidean distance between the forest fragment and the nearest continuous area, in Google Earth software (Google Inc. 2015).

For the two continuous forest sites we attributed a relatively large 'forest fragment' size (400 ha), and a low value of isolation (0 m). Variation in landscape metrics was similar for the forest fragments sampled during the two time periods (1999–2001 and 2005–2009). For the ten forest fragments sampled from 1999 to 2001, habitat amount ranged from 10.5 to 36%, patch size from 13 to 78 ha, patch isolation from 170 to 925 m, and distance to nearest continuous forest from 250 to 8215 m. For the ten forest fragments sampled from 2005 to 2009, habitat amount ranged from 5 to 35%, patch size from 15 to 160 ha, patch isolation from 145 to 1195 m, and distance to nearest continuous forest from 597 to 7724 m.

Local variables

Nine habitat variables were measured to describe aspects of local habitat structure inside forest that could affect species incidence patterns across local communities. All habitat variables were measured within a 3 m radius circle around the center of each trapping station, except for those trapping stations located in the matrix. Six variables were measured qualitatively as present (1) or absent (0) (water course, *Cecropia* spp., lianas, grass, palm *A. aculeatissimum*, and fallen logs), and three were ranked in three levels (1–3; overstory vertical density, understory horizontal density, and tree size). Values recorded at all trap stations of the same forest site were summed, yielding a single value for each variable per site, which was used in subsequent statistical analyses (as in Delciellos et al. 2016). These nine variables were measured once in each site, assuming that the chosen variables do not vary between seasons, or that the variation would not be detected by the sampling method used. Local habitat structure was used as proxy of disturbance related to the history of anthropogenic use of each site, with more disturbed forest sites having higher abundance of lianas, *A. aculeatissimum* palms, trees of the genus *Cecropia*, grasses, reduced overstory vertical density and a more open understory, and predominance of small diameter trees (see Delciellos et al. 2016).

Prior to analysis, the nine habitat variables were standardized and then combined and reduced in a Principal Components Analysis (PCA), using the function *prcomp* in R package *vegan* (Oksanen et al. 2017). The PCA was used to obtain uncorrelated

variables (principal components) that preserve most of the original variation in the data. The number of 'meaningful' principal components was selected by comparing the eigenvalues obtained in PCA to values given by the broken stick distribution (Borcard et al. 2011). For the 12 sites sampled from 1999 to 2001, the first four principal components (PC1 to PC4) were selected, which together explained 91% in data variation (Table 1). The PC1 was associated with sites with increased overstory vertical density, understory horizontal density, abundance of *Cecropia* spp., and abundance of grass; PC2 with decreased tree size and abundance of lianas; PC3 with increased abundance of fallen logs and palms; and PC4 with increased presence of water courses (Table 1). For the ten sites sampled from 2005 to 2009, the first two principal components (PC1 and PC2) were selected, which together explained 67.7% in data variation (Table 1). The PC1 was associated with sites with increased abundance of palms and *Cecropia* spp., and decreased abundance of lianas; and PC2 with decreased tree size and increased overstory vertical density (Table 1).

Spatial variables

A principal coordinate analysis of neighbor matrices (PCNM) was used to evaluate if the environmental gradients structuring the metacommunity were related to the spatial relationships among studied sites, using the function *pcnm* in R package *vegan* (Oksanen et al. 2017). PCNM method consists of a principal coordinate analysis of a truncated pairwise geographic

Euclidean distance matrix between sampling sites (Dray et al. 2006). The chosen threshold to construct the truncated distance matrix was 21.5 km. In this method, only the principal coordinates associated with positive eigenvalues are used as spatial predictors, and retained to be used in further analysis (Dray et al. 2006). Eight positive eigenvectors were selected in the PCNM analyses for the 12 sites sampled from 1999 to 2001, and seven for the ten sites sampled from 2005 to 2009.

Data analysis

We used the analytical methods of Leibold and Mikkelson (2002), and the conceptual framework of Presley et al. (2010), to determine the most likely structure or quasi-structure for the studied metacommunity. The EMS framework is based on the significance of three statistics (coherence, turnover, and boundary clumping), which indicates the most likely pattern of species variation among local communities (Leibold and Mikkelson 2002; Presley et al. 2010). Significance of each statistic was tested with the "r1" moderately-conservative null model (Presley et al. 2010). This null model permutes species incidence across sites 1,000 times, preserving the original species richness of each site, but maintaining their probability of occurrence proportional to their incidence in the original matrix. This permutation procedure avoids that rare species enhance coherence (Presley et al. 2010), and has acceptable levels of type I error (Gotelli and Graves 1996; Presley et al. 2009).

Table 1 Principal components selected from the correlation matrix of habitat structure for the 12 sites sampled from 1999 to 2001 (time period 1) and the 10 sites sampled from 2005 to 2009 (time period 2), in the Macacu River basin, Brazil

The most relevant variables within each component are in bold

Habitat variable	Time period 1				Time period 2	
	PC1	PC2	PC3	PC4	PC1	PC2
Overstory density	**0.464**	− 0.114	0.188	− 0.193	0.217	**0.545**
Understory density	**0.430**	− 0.194	− 0.178	0.339	− 0.359	− 0.187
Tree size	− 0.089	− **0.651**	0.091	0.273	0.249	− **0.517**
Fallen logs	− 0.269	− 0.042	**0.621**	0.027	− 0.330	− 0.399
Lianas	0.234	− **0.627**	0.079	− 0.124	− **0.398**	0.246
Palm	0.238	0.067	**0.538**	− 0.461	**0.434**	0.215
Grass	**0.463**	0.218	0.122	0.030	− 0.215	0.219
Cecropia spp.	**0.439**	0.214	− 0.111	0.195	**0.391**	− 0.128
Water course	0.020	0.179	0.465	**0.711**	0.327	− 0.264
% Variance explained	39.5	20.9	18.8	11.7	47.6	20.1

Reciprocal averaging (Correspondence Analysis, CA) was used to ordinate the species-by-sites incidence matrices. We used incidence rather than abundance matrices because we performed snapshot surveys in all sites (see Field methods section), rather than repeated sampling which is necessary to properly estimate small mammal abundance. The CA maximizes the correspondence between the position of sites and species along the axes based on the degree to which their communities share similar species composition and ranges, respectively, reducing the number of interruptions in species' ranges (Leibold and Mikkelson 2002). Species and sites were ranked according to their position along the primary CA axis.

Coherence was evaluated by counting the number of embedded absences in all species ranges and community composition for each site. Significant negative coherence (i.e. more embedded absences than the null distribution) indicates a checkerboard distribution (Diamond 1975). If coherence is non-significant, the metacommunity is randomly structured regarding the environmental gradient analyzed (Leibold and Mikkelson 2002). A significant positive coherence (i.e. less embedded absence than the null distribution) suggests that species are distributed according to the same gradient (Leibold and Mikkelson 2002), which is further differentiated by evaluating species range turnover and boundary clumping.

Range turnover was calculated by counting the number of replacements, i.e. the number of times a species replaces another at the edge of their ranges (see Presley et al. 2010 for details). The observed number of replacements was then compared to the ones generated by each null metacommunity. A negative or lower number of observed replacements suggest that nestedness (Patterson and Atmar 1986) characterizes the metacommunity structure. If the observed metacommunity exhibits a positive or higher number of replacements, the data are further contrasted by analysis of range boundary clumping. If the range turnover is non-significant the metacommunity exhibits quasi-structures that have the same characteristics as their associated idealized structures, but with weaker structuring processes (see Presley et al. 2010).

In the last step, range boundary clumping was tested using the Morisita's Index, which has an expected value of 1. If the observed index is not significantly different from 1, range boundaries are randomly distributed, indicating a Gleasonian gradient (Leibold and Mikkelson 2002). Conversely, if the observed value is lower or higher than 1, it shows that species range boundaries are overdispersed or clumped, respectively (Leibold and Mikkelson 2002). Nested metacommunities may exhibit clumped, stochastic, or hyperdispersed species loss among sites, which are analogous to Clementsian, Gleasonian and evenly-spaced gradients, respectively, with the difference that these patterns of range dispersion are found only at one side of the distributional gradient (see Presley et al. 2010 for details). Significance of the observed Morisita Index was evaluated using a Chi squared goodness-of-fit test, which compares the observed distribution to an expected distribution of range boundary locations (Presley et al. 2009).

Analyses of EMS were conducted with algorithms written in Matlab R2017b 9.3.0.713579. Site scores for primary CA axes were derived using the function "ca" in Matlab. Script files are available at https://faculty.tarleton.edu/higgins/metacommunity-structure.html. If a positive significant coherence was found, Spearman correlation was used to evaluate the correlation between the site scores for each primary CA axis and the landscape, local, and spatial variables to identify which variables compose the environmental gradient. As the number of sites used in each correlation analysis was relatively low (n = 10 or 12), thus reducing the statistical power of the analysis, we did not perform any adjustment of P-values for multiple comparisons.

We analyzed EMS for three datasets as follows: (1) Humid season for the first time period (HS-1), using the data from 12 sites sampled from 1999 to 2001; (2) Super-humid season for the first time period (SHS-1), using data from 12 sites sampled from 1999 to 2001; and (3) Humid season for the second time period (HS-2), using data from other ten sites sampled from 2005 to 2009 (Online Resource 1—ESM 1). We first compared HS-1 and SHS-1 to evaluate if metacommunity structure varied between climatic seasons. Secondly, we analyzed whether metacommunity structure during a same season (humid) changed between time periods by comparing metacommunity structure during HS-1 and HS-2. All sites sampled the same metacommunity during different time periods and were randomly located across the landscape (Fig. 1). Consequently, each set of sites reflects a representative sample of the metacommunity and

should reflect structure of the metacommunity regardless of the particular sites chosen.

Results

A total of 786 individuals of 19 small mammal species were captured during the first time period (from 1999 to 2001). At the metacommunity level, total species richness and abundance were slightly higher during the HS-1 (399 individuals from 18 species) than during the SHS-1 (387 individuals from 16 species) (Online Resource 1—ESM 2). Species richness across local communities varied from three to 11 species during HS-1 and three to eight species during SHS-1. The metacommunity during the first time period included seven species of marsupials and 12 species of rodents (Online Resource 1—ESM 2). *Akodon cursor* and *Didelphis aurita* were the most abundant species during this first time period. During the second time period (HS-2), 351 individuals of 11 species were captured (Online Resource 1—ESM 2). Species richness across local communities varied from three to seven species. The HS-2 metacommunity included seven species of marsupials and four species of rodents (Online Resource 1—ESM 2). *Philander frenatus* was the most abundant species during this period.

Small mammal metacommunity structure was non-coherent during SHS-1, resulting in a random structure (Table 2), indicating that species did not respond to the same environmental gradient during this season. For both humid periods (HS-1 and HS-2) coherence and turnover were positive and significant, and species

range boundaries were significantly clumped (Table 2). Therefore, the small mammal metacommunity was structured in a Clementsian pattern during each humid season (Table 2).

For HS-1, the PC1 of local habitat structure and patch size were identified as the main variables structuring the metacommunity (Table 3). Positive turnover indicated that sites at opposite ends of the environmental gradient had different species compositions. Sites at one end of the PC1 gradient presented the arboreal *Caluromys philander*, *Guerlinguetus ingrami*, and *Phyllomys* sp. nov., as well as the terrestrial *E. spinosus*, and were associated with increased overstory and understory vegetation, and increased abundance of grass and *Cecropia* spp. (Figure 2). The sites at the opposite end of the gradient were associated with the more terrestrial species *Euryoryzomys russatus*, *Marmosops incanus*, *Monodelphi*s sp., *Oecomys catherinae*, *Oligoryzomys nigripes*, and *Trinomys dimidiatus*, and the arboreal *Phyllomys pattoni* (Fig. 2). Also, some species occurred in larger patches as *E. russatus*, *Monodelphis* sp., *Nectomys squamipes*, *O. nigripes*, *P. pattoni*, and *T. dimidiatus*, whereas *E. spinosus* and *G. ingrami* occurred at the opposite end of gradient (Fig. 3). This ordination suggested the existence of at least two compartments in the metacommunity, the first composed by sites A3–A6, and the second by sites A7, A8, A11 and A12 (Fig. 4a). A third, intermediate compartment may also be identified, which contains mostly generalist species, composed by the remaining sites (Fig. 4a).

For HS-2, the ordination of the species along the first CA axis was related only to patch size variation,

Table 2 Elements of metacommunity structure based on small mammal species-by-site incidence matrices ordinated by the first axis of Correspondence Analysis, for the 12 forest sites sampled from 1999 to 2001 during the super-humid (SHS-1) and humid (HS-1) seasons, and the 10 sites sampled from 2005 to 2009 during the humid season (HS-2), in the Macacu River basin, Brazil

	Coherence				Turnover				Boundary clumping		Structure
	Eabs	*P*	M	*SD*	Re	*P*	M	*SD*.	MI	*P*	
SHS-1	36	0.489	41.18	7.49	–	–	–	–	–	–	Random
HS-1	32	**0.020**	52.55	8.82	349	**0.049**	234.17	58.45	1.84	**0.003**	Clementsian
HS-2	7	**0.029**	17.30	4.71	84	**0.025**	49.16	15.56	2.00	**0.036**	Clementsian

Eabs number of embedded absences, *P* probability value, *M* mean, *SD* standard deviation value for the null distribution, *Re* number of replacements, *MI* Morisita index

Significant values ($P \leq 0.05$) are in bold

Table 3 Spearman correlations between landscape, local (selected principal components of habitat structure) and spatial variables (selected components of the principal coordinate analysis of neighbour matrices) and first axis of correspondence analysis based on species-by-sites incidence matrices for the small mammals metacommunity for the 12 sites sampled from 1999 to 2001 (HS-1) and the 10 sites sampled from 2005 to 2009 (HS-2) during the humid season, in the Macacu River basin, Brazil

Significant values (P ≤ 0.05) are in bold

	HS-1 r	HS-1 P	HS-2 r	HS-2 P
Landscape variables				
Habitat amount (%)	− 0.238	0.456	0.338	0.340
Patch isolation (m)	0.344	0.274	− 0.031	0.933
Patch size (ha)	**− 0.618**	**0.032**	**0.632**	**0.050**
Distance to nearest continuous forest (m)	0.526	0.079	− 0.411	0.238
Local variables				
PC1	**0.781**	**0.003**	− 0.043	0.906
PC2	0.347	0.269	− 0.153	0.672
PC3	0.161	0.617	–	–
PC4	− 0.144	0.656	–	–
Spatial variables				
PCNM1	− 0.144	0.656	0.117	0.748
PCNM2	− 0.095	0.770	− 0.374	0.287
PCNM3	0.441	0.151	0.166	0.647
PCNM4	− 0.203	0.527	− 0.620	0.056
PCNM5	− 0.546	0.066	0.558	0.093
PCNM6	0.207	0.519	0.374	0.287
PCNM7	0.312	0.324	− 0.031	0.933
PCNM8	0.182	0.571	–	–

with *M. nudicaudatus* occurring in the larger patches, and *C. philander*, *E. russatus*, *M. incanus*, and *O. nigripes* occupying the opposite end of gradient (Fig. 5). This indicated the existence of at least two compartments during the HS-2, the first composed by sites B2, B3, and B8, and the second by sites B4 to B6 (Fig. 4b). Again, a third compartment may be identified in between the first two compartments.

Discussion

The structure of the studied small mammal metacommunity is seasonally dynamic, which changes from Clementsian during the humid season to random during the super-humid season. These results corroborate previous studies showing that metacommunity structure is dynamic, rather than constant through time (e.g., Fernandes et al. 2014; Cisneros et al. 2015; Wojciechowski et al. 2017). We also detected a consistency in the Clementsian structure of the metacommunity during humid periods 5 years apart. This consistency occurred even though different sets of sites (forest fragments) were used for the two

periods, indicating that a Clementsian structure does indeed apply to the small mammal community. A cycle in metacommunity structure has rarely been demonstrated, i.e. the returning to the previous idealized structure after the homogenization of structuring environmental gradients. Temporal changes from idealized to random structures have been described for other metacommunities both within and between seasons, and attributed to responses to the homogenization of structuring environmental gradients (Fernandes et al. 2014; Cisneros et al. 2015; Wojciechowski et al. 2017). For example, the change from checkerboard (dry season) to random structure (wet season) of the gleaning animalivore bat metacommunity in a tropical forest was attributed to more abundant prey during the wet season, that reduces competition among species and homogenizes their distribution (Cisneros et al. 2015). Also, a change from idealized to random structure in a metacommunity of phytoplankton was associated with periods of low environmental heterogeneity in limnological characteristics of water in subtropical reservoirs during the spring season of two subsequent years (Wojciechowski et al. 2017). A cycle in metacommunity
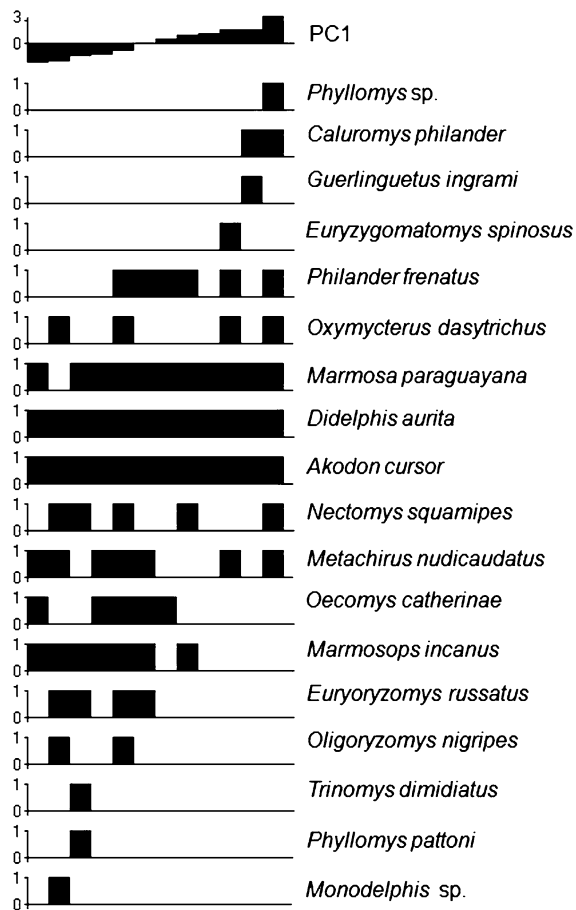
Fig. 2 Ordination of incidence of small mammals along the first principal component (PC1) of habitat structure during the first humid period in 12 sites sampled from 1999 to 2001 in the Macacu River basin, Brazil. PC1 represented a gradient of increased overstory vertical density, understory horizontal density, and abundance of *Cecropia* spp. and grass (from left to right)

Fig. 3 Ordination of incidence of small mammals along a gradient of patch size during the first time period during the humid season in 12 sites sampled from 1999 to 2001 in the Macacu River basin, Brazil. Patch size increased from left to right

structure was also detected for the floodplain-fish metacommunity in the Pantanal of South America (Fernandes et al. 2014). The floodplain-fish metacommunity structure changed from nestedness to quasi-Clementsian throughout the wet season, following the progress of flood levels. During the beginning of the flood season the water level rises, increasing the connectivity and dispersal among habitat patches (Fernandes et al. 2014). The flood-plain fish metacommunity remained structured during the same month (March) across four subsequent years (Fernandes et al. 2014). Similarly, we found consistency in metacommunity structure within a season across time periods for the small mammals.

Variation in functional connectivity between seasons may be a possible explanation for the dynamic cycle in metacommunity structure detected in our study, i.e., the changing from a random to an idealized structure between seasons. The studied forest fragments are embedded in an agricultural matrix, part of which varies in composition between climatic seasons following agricultural activities. The main agricultural products in the studied landscape are corn (*Zea mays*)
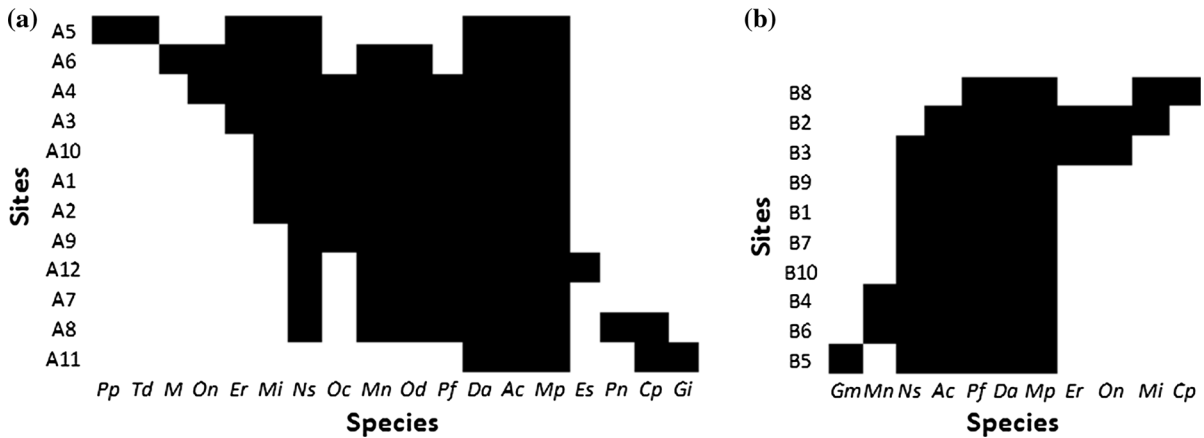
Fig. 4 First axis of the Correspondence Analysis for the matrix of species-by-site incidence of small mammals during the humid season for **a** the 12 sites sampled from 1999 to 2001, and **b** the 10 sites sampled from 2005 to 2009, in the Macacu River basin, Brazil, both revealing a Clementsian metacommunity structure. *Ac = Akodon cursor*, *Cp = Caluromys philander*, *Da = Didelphis aurita*, *Er = Euryoryzomys russatus*, *Es = Euryzygomatomys spinosus*, *Gi = Guerlinguetus ingrami*, *Gm = Gracilinanus*

microtarsus; *M = Monodelphis* sp., *Mi = Marmosops incanus*, *Mn = Metachirus nudicaudatus*, *Mp = Marmosa paraguayana*, *Ns = Nectomys squamipes*, *Oc = Oecomys catherinae*, *Od = Oxymycterus dasytrichus*, *On = Oligoryzomys nigripes*, *Pn = Phyllomys* sp. nov., *Pf = Philander frenatus*, *Pp = Phyllomys pattoni*, *Ri = Rhipidomys itoan*, *Td = Trinomys dimidiatus*
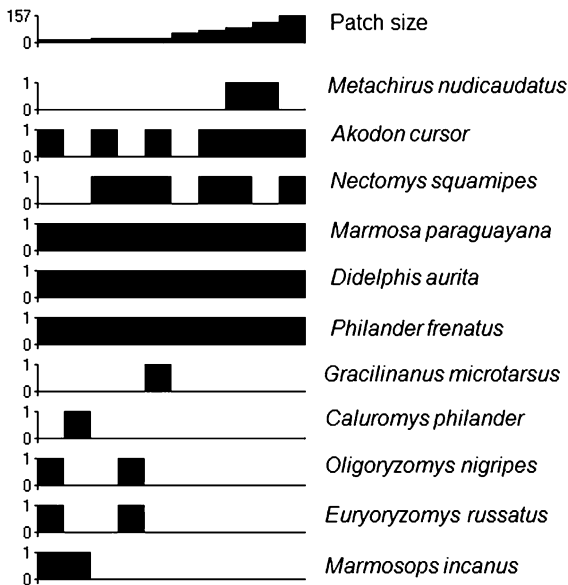

Fig. 5 Ordination of incidence of small mammals along a gradient of patch size during the second time period during the humid season, in the ten sites sampled from 2005 to 2009 in the Macacu River basin, Brazil. Patch size increased from left to right

and cassava (*Manihot esculenta*), which are cultivated from November (beginning of super-humid season) to June (beginning of humid season), when they are harvested (Uzêda et al. 2011). Thus, during more than

half of the humid season, part of the matrix in the landscape is likely to be depleted of any type of vegetation cover. This change in matrix quality may reduce the offer of potentially supplementary (Braga et al. 2015) or complementary (Dunning et al. 1992) resources, and increase exposure of dispersing individuals to predators, thus affecting the movement rates of individuals between forest fragments.

Matrix permeability to movement is generally higher when the matrix is structurally more similar to the habitat patches (Prevedello and Vieira 2010). During the super-humid season, matrix permeability is probably higher than during the humid season, allowing more frequent inter-fragment dispersal. The expected result may be more similar community compositions in different forest fragments, leading to a random pattern of metacommunity structure. On the other hand, when plantations are harvested during the humid season, matrix suitability is likely to decrease and the metacommunity may become structured. The hypothesis that variation in functional connectivity drives the differences in metacommunity structure between seasons may be tested in the future, for example by quantifying inter-fragment movement and functional connectivity during different seasons.

The positive turnover and high and significant Morisita index during both humid seasons indicate

that groups of species are associated with different parts of the environmental gradient in the landscape (Leibold and Mikkelson 2002). These groups form distinct communities from the regional species pool during this season, based on similarities in species habitat requirements or specialization (Leibold and Mikkelson 2002; Presley et al. 2009). Many species of non-volant small mammals of the Atlantic Forest have species-specific habitat requirements (Püttker et al. 2008; Delciellos et al. 2016), thus are likely to vary in their occurrence or abundance in the landscape according to gradients of habitat structure. For example, species of the genus *Akodon* are frequently associated to open habitats, such as natural clearings inside the forest or open matrix habitats where the species is more abundant (e.g., Umetsu et al. 2008), and the semi-aquatic rodent *N. squamipes* is found more frequently or in higher abundance near water courses in forested habitats (e.g., Briani et al. 2001). Also, several species of non-volant small mammals have particular specializations in their diet or locomotion, such as the arboreal marsupial *C. philander*, which has adaptations to locomotion in the forest canopy (e.g., Delciellos and Vieira 2006).

The Clementsian structure detected during the humid season was structured by patch size and habitat structure. Patch size appeared as the only common factor structuring the metacommunity during both time periods (HS-1 and HS-2). Some species were restricted to smaller or larger patches only (see Figs. 3, 5), which may be related to the increased habitat heterogeneity and resource availability in larger forest fragments (Ewers and Didham 2007; Delciellos et al. 2016), and a higher probability of dispersing individuals to find larger patches (Coleman et al. 1982). In addition to patch size, local habitat structure also structured the metacommunity only during the first time period (HS-1). During the HS-1 most species with arboreal and terrestrial habits were found in sites associated to different degrees of complexity of habitat structure. The Clementsian structure detected implies that disturbances acting more strongly on one end of the structuring environmental gradient will affect the group of species of that compartment. For example, deforestation or selective logging inside forest fragments act on the forested end of the gradient, where the compartment composed mostly by arboreal species probably will be the most negatively affected. Habitat structure, considered a proxy

of habitat quality in some studies, is also frequently found as one of the main determinants of species composition for several taxa, such as lepidopterans (Summerville and Crist 2004) and birds (Uezu and Metzger 2011). Our results highlight the importance of local habitat structure for structuring metacommunities of marsupials and rodents in fragmented landscapes.

Climatic seasonality affects the structure of the metacommunity of non-volant small mammals, and both local and landscape factors are important to determine species composition. Our results provide reinforcing evidence that metacommunity structure may be dynamic, rather than constant through time, as previously suggested (e.g., Fernandes et al. 2014; Cisneros et al. 2015). This result has important implications for species inventory and conservation, landscape management, and detection of regional patterns in community structure. First, we suggest that caution is necessary when extrapolating metacommunity patterns detected during snapshot surveys, as metacommunity structure may vary between seasons, at least for non-volant small mammals in agricultural landscapes. Thus, we recommend conducting repeated sampling of local communities in different climatic seasons, whenever possible. Second, we suggest that matrix suitability may determine metacommunity structure even in terrestrial landscapes, as matrix suitability directly affects functional connectivity. There is a growing consensus that management of matrix may be a more feasible and less expensive way to benefit local populations and communities in fragmented landscapes compared to other actions, such as increasing habitat amount (Tscharntke et al. 2012; Driscoll et al. 2013). Here we suggest that management of matrix may also affect metacommunity structure. This suggestion may be tested in future studies by comparing inter-patch dispersal rates and metacommunity structure among landscapes composed of different matrix types or land uses, or at a same landscape during different seasons. Explicit tests of this hypothesis may contribute to identify the underlying mechanisms shaping metacommunity structure in fragmented landscapes, allowing a better understanding of how different anthropogenic activities impact biodiversity.

Data accessibility Data are presented in ESM 1–2.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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