Journal of Insect Conservation (2019) 23:111–121
https://doi.org/10.1007/s10841-018-00120-y

ORIGINAL PAPER

Effects of environmental parameters on beetle assemblage in a fragmented tropical rainforest of South America

Renato P. Salomão[1] · **Lucas C. Brito**[2] · **Luciana Iannuzzi**[3] · **André F. A. Lira**[3] · **Cleide M. R. Albuquerque**[3]

Received: 15 August 2018 / Accepted: 13 December 2018 / Published online: 23 January 2019

Abstract

As a result of habitat fragmentation, the environmental structures of forest remnants change and alter their microclimatic conditions. Edaphic beetles comprise several families that are considered effective bioindicators. In this study, we analyzed how environmental parameters and fragment size affect edaphic beetle assemblage in a fragmented rainforest landscape in Brazil. Beetles were sampled in 12 forest fragments using pitfall traps. Fragment size, tree density and diameter, litter depth and dry weight, and canopy cover were measured in each forest fragment. Staphylinidae and Carabidae were the beetle families with the highest species richness, whereas Scarabaeidae and Nitidulidae were the most abundant families. Beetle abundance was positively affected by litter dry weight and fragment size. In addition, species composition was significantly affected by fragment area. In conclusion, forest patch size is an important parameter for maintaining edaphic beetle assemblages in tropical rainforests, causing major shifts in its abundance and species distribution.

Keywords Bioindicator · Edaphic Coleoptera · Environmental disturbance · Habitat structure

Introduction

Loss of biodiversity as a consequence of loss and fragmentation of native habitats has been observed frequently in tropical forests (Saunders et al. 1991; Myers et al. 2000; Haddad et al. 2015). Regarding habitat fragmentation, fragment size is one of the most important drivers of change in ecological communities, and smaller fragments are more prone to rapid decreases in biodiversity, compared to larger forest patches (Santos et al. 2008; Leal et al. 2012; Haddad et al. 2015). With the reduction of native areas, patch attributes (e.g., fragment size) and landscape parameters (e.g., connectivity and matrix type) affect environmental structure of the forest patches and therefore modify the microclimatic conditions (Bennet and Saunders 2010; Haddad et al. 2015). Habitat configuration of forest patches may threaten the native communities (Nichols et al. 2007; Haddad et al. 2015; Boscolo et al. 2017), and litter volume, tree diameter, height and density, and canopy openness are important characteristics that vary between forest fragments (Lira et al. 2015; Ezcurra 2016). Furthermore, abiotic parameters such as temperature, humidity, and light incidence also differ between patches, mainly due to forest edge effects, which are stronger in smaller than in larger forest fragments (Turner 1996; Ranta et al. 1998; Harper et al. 2005; Herrmann et al. 2005; Magnano et al. 2015).

Among insects that inhabit forest fragments, edaphic beetles represent a group that present strict associations with microclimatic conditions and that are highly susceptible to habitat changes (Pearson and Cassola 1992; Barbosa et al. 2002; Nichols et al. 2007; Fagundes et al. 2011; Wardhaugh et al. 2013). Edaphic beetles exhibit distinct feeding habits and can be classified as detritivores, saprophages, predators, or herbivores, and are represented mostly by species of the

---

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10841-018-00120-y) contains supplementary material, which is available to authorized users.

✉ Renato P. Salomão
renatopsalomao3@hotmail.com

[1] Red de Ecoetología, Instituto de Ecología A. C., Carretera Antigua a Coatepec, 351, El Haya, 91070 Xalapa, Veracruz, Mexico

[2] Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos, Instituto de Ciências Biológicas e da Saúde, Universidade Federal de Alagoas, Av. Lourival Melo Mota, S/N, Maceió, Brazil

[3] Programa de Pós-Graduação em Biologia Animal, Depto de Zoologia, Universidade Federal de Pernambuco, Av. Prof. Moraes Rego, S/N, Recife, PE, Brazil

families Carabidae, Scarabaeidae, and Staphylinidae (Didham et al. 1998a; Barbosa et al. 2002; Lassau et al. 2005). Responses of such insects are associated with their environmental tolerance and their foraging strategies (Didham et al. 1998a; Larsen et al. 2006; Fagundes et al. 2011; Wardhaugh et al. 2013). Some species of edaphic beetles thrive in either disturbed or conserved habitats whereas other species are habitat generalists (Rodríguez et al. 1998; Fagundes et al. 2011). Moreover, some edaphic beetles prefer wet conditions and inhabit sites with closed canopy cover and higher leaf litter amount, whereas other species occur at dry and more exposed sites (Barbosa et al. 2002; Grimbacher and Catterall 2007; Fagundes et al. 2011).

Among edaphic beetles, numerous families are considered reliable bioindicators (Halffter and Favila 1993; Rodríguez et al. 1998; Maleque et al. 2009), which help understand the trends of ecological communities under habitat disturbances (Noss 1990). However, the responses of beetle assemblages facing habitat disturbances may differ between indicator groups at different taxonomic levels (Basset et al. 2004). Studies on indicator species and populations can provide important information for decisions on the conservation status of an ecosystem (Noss 1999; Stem et al. 2005; Beaupre and Douglas 2009). When analyzing effects of disturbances on ecological communities, assessments on a broader scale (e.g., a set of various indicator families) may produce a more informative picture than that by assessments based on a single family or an entire phylum (Basset et al. 2004).

Through the understanding of community structures based on indicator groups, it is possible to predict trends in biodiversity (Noss 1990; Rimbach et al. 2013; Alves and Hernández 2017). Furthermore, alterations in community structure due to habitat changes can directly and indirectly affect the ecological stability and, consequently, influence ecosystem services for human well-being (Bennet and Saunders 2010; Haddad et al. 2015). Evidence suggests that edaphic beetles perform crucial ecological services that are undoubtedly associated with ecosystem functioning. For example, decomposers and predators are involved in several trophic interactions, which makes them important for nutrient cycling and parasite control (Didham et al. 1998a; Lassau et al. 2005; Losey and Vaughan 2010).

The Atlantic rainforests are neotropical ecosystems that occur mainly along the coastal regions of Brazil. The northern Atlantic rainforest is an important endemism center (Pernambuco Endemism Center—CEPE) and is considered a hotspot for global conservation because of the high levels of endemism and the substantial loss of native vegetation (Prance 1987; Myers et al. 2000; Silva and Casteleti 2003). Intensive agriculture in the north Atlantic rainforest since the sixteenth century produced a highly fragmented landscape, with a coverage reduction to currently ca. 12% (Ribeiro et al. 2009). Fragment configuration, edge effects, and canopy openness are known to affect dung beetle assemblages in the CEPE (Filgueiras et al. 2011; Costa et al. 2013). Based on these findings, our main objective was to analyze how environmental parameters and fragment size affect edaphic beetle assemblages. Specifically, we assessed the effect of micro-environmental characteristics (i.e., tree density and diameter, canopy openness, and litter depth and dry weight) and fragment size on beetle abundance, species richness, species composition and diversity. Regarding the specific habitat requirements of Coleoptera species that inhabit tropical forests, we hypothesized that environmental parameters and fragment size should affect beetle assemblage structure. Ecosystems that have complex vegetation structures with high plant density and high amounts of litter may indicate high resource availability, which should positively affect the abundance of animal assemblages that depend on the vegetation environment to feed and to find food (e.g., herbivores, predators, and detritivores) (Cuevas-Reyes et al. 2004; Sayad et al. 2012; Lira et al. 2015). Therefore, we predicted that increasing tree density and diameter and increasing litter depth and dry weight should positively affect edaphic beetle abundance. A more open canopy may be associated with a less complex vegetation structure (Sarges et al. 2012); however, it also favors the establishment of beetle species that depend on greater light exposure (Didham et al. 1998a; Karen et al. 2008). Based on the intermediate disturbance hypothesis (Connel 1978), we expected higher species richness, abundance, and diversity of edaphic beetles in forest fragments with a more open canopy than in fragments with closed canopy. As larger fragments may comprise more microhabitats than that in smaller fragments (Fleury and Galetti 2006) and, thus, present higher resource availability, we expected fragment size to positively affect edaphic beetle abundance, species richness, species composition and diversity.

Materials and methods

Study site

This study was conducted in 12 forest fragments (from 6 to 469 ha) (Fig. 1, Table in the Supplementary Material), all of which were surrounded by sugarcane plantations, which were subjected to annual management cycles involving slash-and-burn practices. Forest patches are located in Usina Trapiche (08°35′S; 35°06′W), which is situated in the municipality of Sirinhaém, Pernambuco state, Brazil (Fig. 1). The region has a tropical rainy climate with a mean annual precipitation of 2400 mm and a mean annual temperature of 25 °C (Silva et al. 2010). The forest fragments had dense ombrophilous vegetation and are situated on top of hills below 100 m a.s.l.

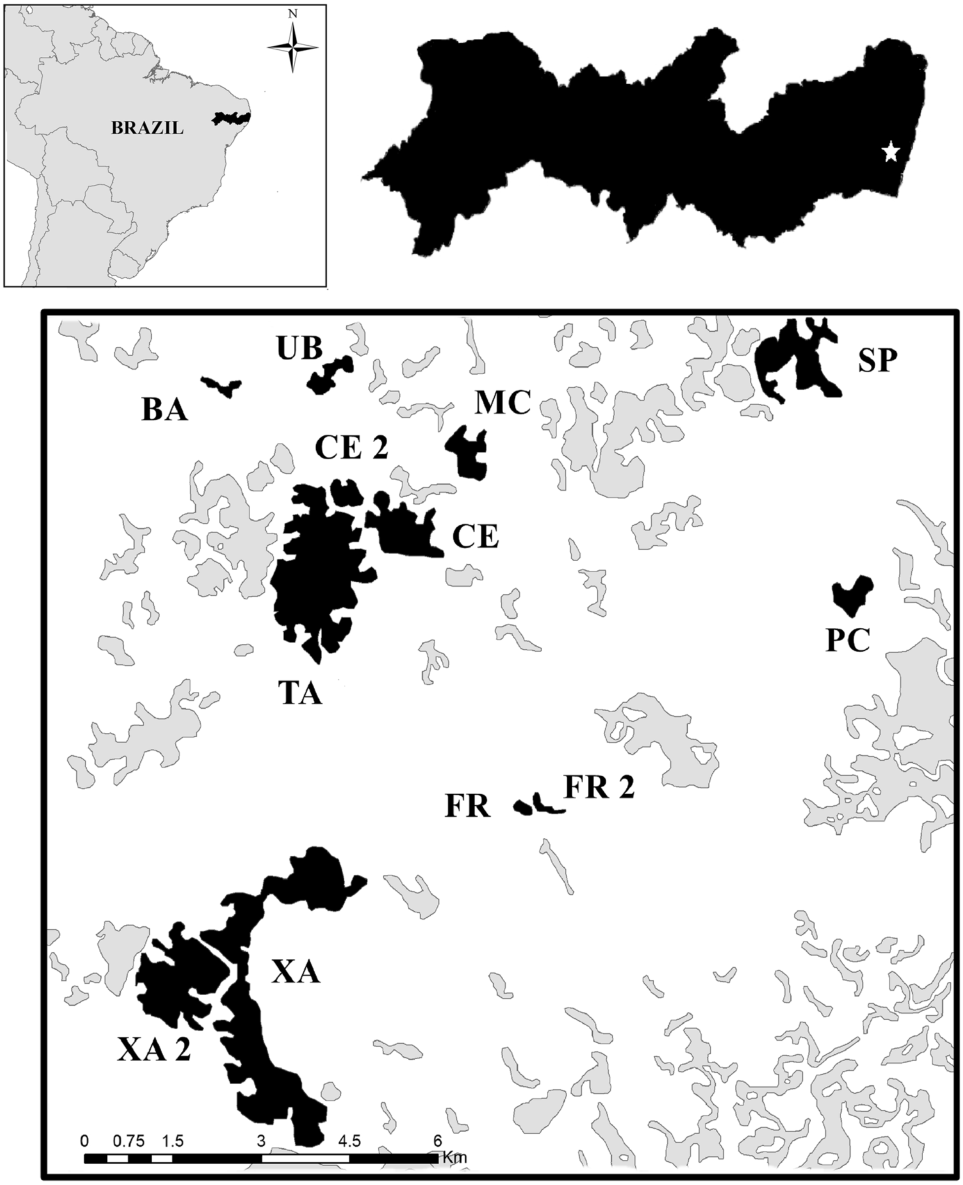

Fig. 1 Map of the sampled forest fragments (in dark-gray) and the location of the sampling site in Usina Trapiche, Pernambuco, Brazil. *UB* Ubaca, *BA* Baquinha, *XA* Xanguá, *XA2* Xanguá2, *SP* São Pedro, *CE* Canto Escuro, *CE2* Canto Escuro2, *FR* Franco, *FR2* Franco2, *MC* Mata das Cobras, *PC* Pedra do Cão, *TA* Tauá

Beetle sampling

Beetles were sampled during the dry season of the year (December 2012 and January 2013), period when there were no burning activities in the sugarcane plantations. Samples were collected only during the dry season because there is no clear distinct seasonality in beetles (specifically Scarabaeidae) in this region of the Atlantic rainforest (Filgueiras et al. 2009; Iannuzzi et al. 2016). Beetles were collected using pitfall traps, which consisted of a cylindrical plastic container (15 cm diameter × 13 cm height) containing 70% alcohol (250 ml) to preserve the collected material. In each fragment, four 40-m long linear transects were stablished at 20 m distance from each other, located ca. 200 m from the forest edge toward the forest core in order to reduce edge effects (Hill et al. 2011). In each transect, five traps were placed at 10 m distance from each other, and thus, 20 traps were used per forest fragment. Traps were left for 5 days after which beetles were collected and stored in 70% alcohol. In the laboratory, all beetles were identified at family level (taxonomic keys from Downie and Arnett 1995; Arnett et al. 2002; Rafael et al. 2012). After this, the beetles were morphotyped and, if possible, identified to species level. The identified specimens were deposited in the Coleção Entomológica da Universidade Federal de Pernambuco (CE-UFPE).

Environmental parameters

Habitat structure was analyzed based on the methods used by Lira et al. (2015), considering five micro-environmental characteristics: tree density, tree diameter, litter depth, litter dry weight, and canopy cover. In addition, the respective size of each forest fragment was recorded using digital maps. Tree density was measured as the number of trees and shrubs that touched the linear sampling transects. Tree diameter was measured at breast height (DBH), using trees that were included in the tree density measurements. For both tree density and tree diameter, mean values were produced for each transect. Litter depth was measured in three random 25 cm^2 squares per fragment, placed at the soil surface, and the litter depth of each peak of the square was measured using a ruler. Litter dry weight was recorded using three random litter samples (25 × 25 cm) from sites at 10 m distance from each other in each transect. The litter samples were dried at 50 °C for 48 h, and the dry mass was weighted using a balance DCR CL-LB, with a precision of 100 g. Canopy cover was estimated using hemispherical photographs taken using a Nikon Coolpix E4500 camera with a Nikon FC-E8 lens. One photography was taken in the center of each transect, and the photographs were analyzed using Gap Light Analyzer software version 2.0 (Frazer et al. 1999). The photographs were taken at times of diffuse light, between 5:00 and 6:00 h.

Data analyses

To assess sampling efficiency in the studied forest fragments, we used species accumulation curves. We used the estimators of species richness Jackknife 1, Jackknife 2, Chao 1, and Chao 2 based on the number of samples (i.e., forest fragments) to compare beetle species richness between forest fragments. Rarefaction and extrapolation curves were produced using the nonparametric methods of Colwell et al. (2012). These analyses were performed using Estimates software version 9.1.0 (Colwell 2013).

Dichotomius iannuzziae Valois et al. (2017) as dominant in the Coleoptera assemblage, representing more than half of the collected beetles. Therefore, we performed data transformation on similarity matrices. In addition, we fitted models with and without this species to test its importance for the effect of environmental parameters and fragment size on beetle assemblage.

To analyze beetle diversity in forest fragments, we used components of diversity, considering alpha (Dα), beta (Dβ), and gamma (Dγ) diversities (Jost 2006). We evaluated the components of diversity using Hill numbers, using the number of species (0D) and Shannon diversity (1D) (Hill 1973; Jost 2006). 0D assigns higher weight to rare species than 1D, which considers the relative species abundance. 0Dα indicates the mean number of species per forest fragment, whereas 1Dα represents the number of abundant species of the patches. Beta diversity indicates the species turnover within the landscape, based on species richness (0Dβ) and relative species abundance (1Dβ). 0Dγ indicates the total number of species in the study, and 1Dγ indicates the number of abundant species. We calculated diversity numbers according to Marcon and Hérault (2015), which provides a bias correction for incomplete sampling. Statistical analyses were conducted using the entropart package in R software version 3.2.0 (R Core Team 2015; Marcon and Hérault 2015).

To analyze whether environmental parameters and fragment size affected observed and expected beetle species richness and abundance, we fitted generalized linear models (GLM) with a negative binomial distribution (to analyze abundance), a Poisson distribution (to analyze species richness), and a Gaussian distribution (to analyze estimated species richness). Estimated species richness was obtained using the estimator Chao 1, which is recommended for assemblages with many rare species, similar to what we found in this study. The effects of tree density, DBH, canopy openness, litter depth, litter dry weight, and forest fragment size on beetle abundance and species richness were tested. The models used to analyze the dependent variables were reduced based on the Akaike Information Criteria (AIC). The variables that were excluded in the most parsimonious models were considered non-significant. The significance of the dependent variables was tested using a likelihood ratio test between the full and the reduced model using the lmtest package (Zuur et al. 2009; Hothorn et al. 2018). Normality of the residuals was visually assessed from normal q–q plots, and the presence of outliers was tested using Cook's distance. GLMs for beetle abundance were conducted with and without the data of the dung beetle *D. iannuzziae*. All analyses were performed using R software version 3.2.0 (R Core Team 2015).

We used principal coordinates of neighbour matrices (PCNM) from the geographical distance matrix (coordinates in decimal degrees) to generate spatial variables. This method partitions the spatial dataset structure in eigenfunctions that can be used as variables of the spatial structure (Bocard and Legendre 2002; Dray et al. 2006). These spatial variables were used to assess the effects of the spatial arrangement of forest fragments (connectivity) on the beetle assemblage similarity (species richness and composition) using a redundancy analysis (RDA). The significance of each variable was calculated using a partial Monte Carlo test with 9999 permutations. All analyses were performed using the vegan package in R software version 3.2.0 (R Core Team 2015; Oksanen et al. 2018).

Correlations between beetle assemblage compositions (with and without *D. iannuzziae* data) and the environmental factors were calculated using an RDA with a ‘manual selection’ of independent variables in the CANOCO software version 4.5 (ter Braak and Smilauer 2003). The RDA allows testing the effect of each factor on species composition as the only explanatory variable (Leps and Smilauer 2003). In this analysis, linear combination of the species abundance and the environmental variables were fitted, and the significance of each variable was calculated using a partial Monte Carlo test with 9999 permutations (Legendre and Legendre 1998; McCune and Grace 2002; Leps and Smilauer 2003). Linear responses of changes in the species composition were confirmed using a detrended correspondence analysis prior to the RDA (lengths of gradients = 2.77) (Leps and Smilauer 2003).

In the RDA and GLMs, correlations between environmental variables were assessed using the variance inflation factor (VIF) calculated using CANOCO software version 4.5 (ter Braak and Smilauer 2003). VIF values > 10 indicated that the variance of the canonical coefficients was inflated by multicollinearity of the explanatory variables and produced instability of the regression model (ter Braak and Smilauer 2003; Kutner et al. 2005; Zuur et al. 2009).

Results

A total of 1701 beetles belonging to 65 species and 14 families were collected. According to Chao 1 and Chao 2, the samplings performed in forest fragments recorded 46.30% and 33.52%, respectively, of the expected species. According to Jackknife 1 and Jackknife 2, the samplings recorded 65.11% and 50.59%, respectively, of the expected species. Staphylinidae and Carabidae were the families with most species (s = 14 and 10, respectively), which together comprised 36.92% of the total number of observed species (Table 1). Scarabaeidae and Nitidulidae were the families with the highest abundance of collected beetles (n = 1184 and 225), together representing 82.83% of the total number of collected individuals. Erotylidae and Mordellidae were represented by only one species each, being both singletons (Table 1). In addition, more than half of the species observed in the current study were singletons (s = 33), and six species were doubletons (see in Supplementary Material).

Dichotomius iannuzziae, Scarabaeidae sp1 and Nitidulidae sp1 were the most abundant species, accounting for 69.49% of the collected individuals (Fig. 2). The region of Usina Trapiche presented approximately 17 species per fragment (0Dα = 17.18), with nearly four abundant species per forest patch (1Dα = 3.98). In the whole region, almost eight species were considered abundant (1Dɤ = 7.98). Beta diversity based on beetle richness indicated four distinct beetle assemblages in the 12 sampled forest fragments (0Dβ = 3.78), whereas two distinct assemblages were observed based on Shannon diversity (1Dβ = 2.00).

The degree of collinearity between the explanatory variables of both RDA and GLM were low (VIF = 1.79–4.26), indicating no problems related to data multicollinearity. In the analysis with *D. iannuzziae* (the most abundant beetle species), beetle abundance was explained best by litter dry weight and fragment size (Table 2). Abundance was positively correlated with litter dry weight (Fig. 3a) and fragment size (Fig. 3b). In the analysis without *D. iannuzziae*,

Table 1 Abundance and species richness of beetle families collected in Atlantic forest patches in Usina Trapiche, Pernambuco, Brazil

	Forest fragments												N	S
	FR1	FR2	BA	CE2	UB	PC	CE1	MC	SP	XA2	TA	XA1		
Bostrichidae	0	0	1	0	2	0	1	1	1	0	4	0	10	2
Carabidae	9	4	2	12	3	3	4	5	5	3	2	5	47	10
Chrysomelidae	2	1	1	1	0	0	2	0	1	1	0	9	18	5
Curculionidae	1	0	1	2	1	0	2	0	4	1	0	2	13	7
Dermestidae	2	0	0	0	1	2	0	0	2	11	5	8	31	1
Elateridae	1	2	3	3	0	0	1	0	0	0	0	3	12	7
Erotylidae	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Mordellidae	0	0	0	0	0	0	1	0	0	0	0	0	1	1
Nitidulidae	26	10	17	35	27	24	37	15	3	6	3	22	225	3
Pselaphidae	0	0	1	0	0	0	1	2	0	0	0	0	4	1
Scarabaeidae	43	1	77	14	37	0	19	11	334	371	34	224	1184	5
Scymaenidae	2	0	0	0	0	0	0	0	0	0	0	0	2	1
Staphylinidae	1	1	18	20	11	0	23	6	4	29	6	10	129	14
Tenebrionidae	0	0	7	2	0	4	1	0	0	5	1	4	24	7

UB Ubaca, *BA* Baquinha, *XA* Xanguá, *XA2* Xanguá2, *SP* São Pedro, *CE* Canto Escuro, *CE2* Canto Escuro2, *FR* Franco, *FR2* Franco2, *MC* Mata das Cobras, *PC* Pedra do Cão, *TA* Tauá, *N* total number of collected beetles, *S* number of species

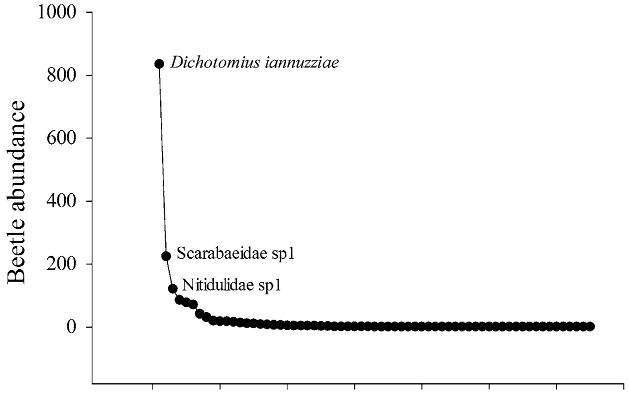

Fig. 2 Rank-abundance curves of beetle species sampled in forest patches in Usina Trapiche, Pernambuco, Brazil

beetle abundance was explained best by tree density and litter depth; however, these factors did not significantly affect beetle abundance (Table 2). Observed beetle richness was better explained by tree density, but there was no significant effect over richness (Table 2). However, estimated beetle richness was positively affected by tree density (Table 2; Fig. 3c).

Beetle species richness and composition was not influenced by the spatial arrangement of the forest fragments, according to the RDA (richness: F = 2.86, p = 0.171; composition: F = 1.30, p = 0.056). In the analysis with *D. iannuzziae*, the environmental variables explained 84.5% of the variability of species composition, of which 95.6% was explained by axis 1 and 2.8% by axis 2 of the RDA. Only fragment area was correlated with the beetle composition, according to the RDA (Table 3). The patch area explained ca. 36% of the species composition variability (RDA: F = 9.55; p = 0.026). When data were analyzed without *D. iannuzziae*, the variation of species composition was explained to 74% by environmental variables, of which 42.4% was represented by axis 1 and 16.9% by axis 2 of the RDA. Forest fragment area (RDA: F = 3.06; p = 0.038) and litter depth (RDA: F = 3.03; p = 0.035) together explained 39% of the species composition variation (Table 3).

Discussion

Beetle communities comprise species that are vulnerable to habitat disturbance, and others that are eurytopic, and can thus occupy habitats with varying environmental structures (Didham et al. 1998a; Rodríguez et al. 1998; Rainio and Niemelä 2003; Nichols et al. 2007; Fagundes et al. 2011). In the present study, both the environmental parameters and forest fragment size affected beetle assemblages in a north Atlantic rainforest. Due to the natural diversity and heterogeneity of tropical rainforests, larger forest patches are assumed to represent more complex habitats, providing high microhabitat diversity for beetle species (Bierregaard et al. 1992; Turner 1996). As a consequence, large patches provide a wider array of resources and therefore facilitate high species diversity of edaphic beetles.

Scarabaeidae and Nitidulidae were the most abundant families in the current study. This result is related to the dominance of a few species of these families. For example, the dominant species in the current study, *D. iannuzziae*, is widely dominant in forest fragments of north Atlantic rainforest and occurs in both disturbed and conserved patches (Filgueiras et al. 2011; Costa et al. 2013; Salomão and Iannuzzi 2015). Although this species was described only recently, it was previously referred to as *D.* aff. *sericeus* and was observed in the Atlantic forest of northeastern Brazil (see Valois et al. 2017). Similarly, there are Nitidulidae beetles that are highly abundant in some areas due

Table 2 Generalized linear models to test the effect of environmental variables and forest fragment size on observed and estimated species richness and abundance of beetles in Atlantic forest fragments in Usina Trapiche, Pernambuco, Brazil. The environmental variables DBH and canopy openness were removed from this table as they did not significantly affect beetle species richness and abundance

Estimated species richness	df	F	St. error	p	Effect size (R^2)
Tree density	**1,10**	**211.53**	**1.190**	**0.037**	**0.301 (+)**
Observed species richness					
Tree density	1,10	2.298	0.045	0.129	0.200
Abundance with *D. iannuzziae*					
Litter dry weight	**1,10**	**7.110**	**1.609**	**0.007**	**0.297 (+)**
Fragment size	**1,9**	**11.169**	**0.001**	**< 0.001**	**0.263 (+)**
Abundance without *D. iannuzziae*					
Tree density	1,10	0.545	0.095	0.460	0.044
Litter depth	1,9	1.277	0.061	0.258	0.020

Models of abundance were fitted with and without the most abundant species (*Dichotomius iannuzziae*). Variables that were statistically significant are shown in bold

"+" indicates a positive relation

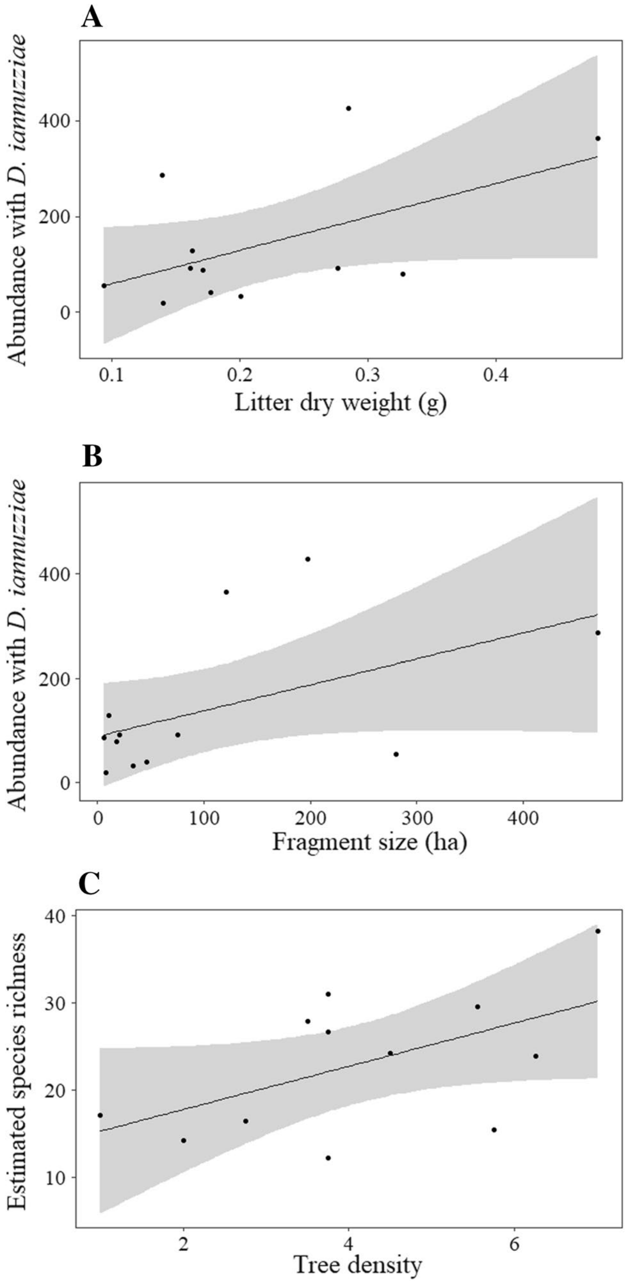

Fig. 3 Relationship between environmental parameters and beetle assemblage: beetle abundance (with *Dichotomius iannuzziae*) and litter dry weight (**a**) and fragment size (**b**); estimated beetle richness and tree density (**c**)

to their successful association with specific food resources (e.g., plant matter, fruits, pollen, or honey) (Barbosa et al. 2002; Aguirre and Dirzo 2008; Fagundes et al. 2011). In addition, Staphylinidae and Carabidae were the most diverse families in the current study. These families are diverse in conserved and disturbed environments, both in tropical and temperate ecosystems (Didham et al. 1998b; McIntyre 2000; Lassau et al. 2005; Buddle et al. 2006; Salomão et al. 2018).

Table 3 RDA of beetle richness and species composition constrained by environmental variables in Atlantic forest fragments in Usina Trapiche, Pernambuco, Brazil

Environmental variable	Variation explained (%)	F	p
With *D. iannuzziae*			
Litter dry mass	30	4.22	0.064
Remnant area	36	9.55	0.026
Canopy cover	4	1.71	0.198
Litter depth	1	0.32	0.713
DBH	12	4.38	0.059
Tree density	2	0.43	0.623
Without *D. iannuzziae*			
Litter dry mass	14	2	0.134
Remnant area	16	3.06	0.038
Canopy cover	3	0.57	0.680
Litter depth	23	3.03	0.035
DBH	6	1.22	0.326
Tree density	12	1.93	0.128

Furthermore, Staphylinidae and Carabidae were already shown to occur at high diversity in Amazon and north Atlantic rainforest (Didham et al. 1998b; Salomão et al. 2018). The north Atlantic forest is a highly fragmented landscape and typically experiences strong edge effects (Ranta et al. 1998). This may be favoring high species richness of Staphylinidae and Carabidae, and its assemblage may be dominated by species that successfully occupy conserved and disturbed habitats. Based on these results, we suggest that Staphylinidae, Carabidae, Scarabaeidae, and Nitidulidae are good indicators of landscape fragmentation in the north Atlantic rainforest.

The sampling effort in this study was similar to that of other studies of insect diversity in tropical rainforests (Moeed and Meads 1985; Lassau et al. 2005; Fagundes et al. 2011), however, the relatively low sampling efficiency must be considered (see Brehm et al. 2005; Rocha-Ortega and Favila 2013; Hernández et al. 2014). This survey was conducted only during the dry season. Thus, additional sampling during the rainy season, which is the time of highest insect activity in most tropical ecosystems (Wolda 1978, 1989; Tanaka and Tanaka 1982; Vasconcellos et al. 2010, but see), could potentially improve the sampling efficiency. However, previous diversity surveys in the same ecosystem did not produce substantial differences between the rainy and dry seasons regarding beetle diversity (i.e. Scarabaeidae; see Filgueiras et al. 2009; Iannuzzi et al. 2016). Although low sampling efficiency may indicate insufficient surveying to assess biodiversity, it is important to consider the huge number of rare insect species in tropical rainforests (Novotny and Basset 2000), as confirmed by the high number of singleton and doubleton species in the present study. This factor seems to be a determinant of the low sampling efficiency of the current study, where the majority of the recorded species were rare. In addition, this may be a result of using an entire order of insects as a focal group and using a sampling method which captured beetles that randomly fell in the traps. Therefore, we suggest that increased sampling effort is necessary to achieve sufficient sampling efficiency of the edaphic beetle fauna in north Atlantic rainforest fragments.

Beetle abundance was positively correlated with litter dry weight, and fragment size affected beetle assemblage structure, abundance, and species composition. Edaphic beetles included the group Coleoptera that mainly thrives in litter and therefore depends on the condition of this habitat. Invertebrate communities that inhabit the litter layer use this habitat as shelter and food resource (Sayad et al. 2012; Luz et al. 2013). Ecosystems with thicker litter layers may therefore be more suitable for more abundant edaphic community, due to the higher habitat availability (Sayer et al. 2010; Sayad et al. 2012). However, apparently few species seem to benefit particularly from this increased habitat space, as there was no significant correlation between litter dry weight and species richness. Besides the amount of litter, the microhabitat condition and the plant composition of litter typically affect the distribution of litter-dwelling beetles (Magura et al. 2004; Vanderwall et al. 2006; Wiezik et al. 2007). Therefore, we suggest that such environmental parameters may result in synergistic effects influencing the distribution of litter-dwelling beetles in the soil. Further studies are needed to assess how litter parameters (e.g., quality, plant species, microhabitat characteristics, and suitability as a food resource) affect beetle distribution in tropical forests.

Fragment size significantly affected beetle community structure. Larger forest patches presented a more abundant beetle fauna and a distinct species composition, compared with smaller forest fragments. Previous studies attributed larger forest patch size to higher habitat availability, which thus favors more individuals and different species, compared with smaller fragments (Bennet and Saunders 2010; Haddad et al. 2015). In addition, the more representative families belonging to the Coleoptera in the current study (i.e., Staphylinidae, Carabidae, Scarabaeidae and Nitidulidae) are sensitive to habitat fragmentation with shifts in their communities according to fragment size and environmental structure (Didham et al. 1998a; Rainio and Niemelä 2003; Nichols et al. 2007; Fagundes et al. 2011). Tropical rainforest are heterogeneous landscapes, comprising myriads of different microhabitats, which favors high insect biodiversity (Wilson 1988; Larsen et al. 2006; Novotny et al. 2006). Due to the high fragmentation of tropical rainforests, recent studies are presenting alarming scenarios with a considerable loss of biodiversity (Myers et al. 2000; Santos et al. 2008; Tabarelli et al. 2012). Based on the results of the current study, we suggest that patch size is one of the main drivers of changes in beetle community structure in fragmented landscapes. It is unclear whether there is higher microhabitat diversity in larger Atlantic rainforest patches than in smaller fragments, as no correlation between environmental parameters and fragment size was observed. Thus, further studies are needed to test this hypothesis.

Species dominance affects species coexistence, which may affect metacommunity dynamics and ecosystem properties (Hooper et al. 2005; Hillebrand et al. 2008). Interestingly, the analyses conducted with and without the dominant species of the current study (*D. iannuzziae*) presented contrasting results regarding the response of edaphic beetle assemblage to environmental parameters and fragment size. In the current study, the weighting of each species was either considered independently (e.g. Mantel, NMDS), or the overall abundance of the edaphic beetles was used (e.g. GLM). Thus, the weighting of a superabundant species such as *D. iannuzziae*, which was almost fourfold more abundant that the second most abundant species, may bias results that are abundance-dependent. Our results suggest that dominant species affect responses of ecological assemblages to environmental parameters. Thus, analyses encompassing assemblages must be interpreted with care, considering the statistical bias that may be introduced by dominant species, such as *D. iannuzziae*. Future studies on assemblages with superabundant species should consider their responses by using analyses with and without such taxa to achieve a more precise and detailed interpretation of assemblage responses.

With this study, we demonstrate that forest fragment size and micro-environmental characteristics significantly affected edaphic beetle community. Habitat loss in north Atlantic rainforests has led to a substantial loss in species richness and abundance, and produced a turnover in species composition of edaphic beetles. Considering that the most diverse and abundant beetles of this landscape are decomposers and predators, the decrease of patch area and modification of environmental structure may induce drastic changes in the nutrient cycling process and in community dynamics.

Acknowledgements We thank to Trapiche sugarcane processing plant for infrastructure, logistic support, and for authorizing our fieldwork. We would like to thank M Hernández-López for comments on earlier versions of the manuscript and to AM DeSouza for their statistical assistance. We also thank "Coordenação de Aperfeiçoamento de Pessoal de Nível Superior" (CAPES) for a doctoral scholarship to AFA Lira and a master's scholarship to LC Brito. We also thank "Consejo Nacional de Ciencia y Tecnología" (CONACYT) for a doctoral scholarship to RP Salomão and "Conselho Nacional de Desenvolvimento Científico e Tecnológico" (CNPq) for providing PQ2 research grant (Fellowship #307759/2015-6) to CMR Albuquerque.

Compliance with ethical standards

Conflict of interest The experimentation was non-invasive and complied with Brazilian law (SISBIO/ICMBIO Permit Number: 1982628). At the end of the experiment, the specimens were deposited in the Entomological Collection of the Universidade Federal de Pernambuco following standard procedures, and there are no conflicts of interest (financial and non-financial).

Research involving human and animal participants No human participants were used in this study; thus, no informed consent was required.

References

Aguirre A, Dirzo R (2008) Effects of fragmentation on pollinator abundance and fruit set of an abundant understory palm in a Mexican tropical forest. Biol Conserv 141:375–384

Alves VM, Hernández MIM (2017) Morphometric modifications in *Canthon quinquemaculatus* Castelnau 1840 (Coleoptera: Scarabaeinae): sublethal effects of transgenic maize? Insects 115:1–10

Arnett RH, Thomas MC, Skelley PE, Frank JH (2002) American beetles, volume II: polyphaga: Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton

Barbosa MGV, Fonseca CRV, Hammond PMH, Stork NE (2002) Diversity and similarity between habitats based on the leaf litter Coleoptera fauna from the terra firme forest of Central Amazonia. Monografías Tercer Milenio 2:69–83

Basset Y, Mavoungou JF, Mikissa JB, Missa O, Miller SE, Kitching RL, Alonso A (2004) Discriminatory power of different arthropod data sets for the biological monitoring of anthropogenic disturbance in tropical forests. Biodivers Conserv 13:709–732

Beaupre SJ, Douglas LE (2009) Snakes as indicators and monitors of ecosystem properties. In: Mullin SJ, Seigel RA (eds) Snakes: ecology and conservation. Cornell University Press, New York, pp 244–261

Bennett AF, Saunders DA (2010) Habitat fragmentation and landscape change. In: Sodhi NS, Ehrlich PR (eds) Conservation biology for all. Oxford University Press, Oxford, pp 88–106

Bierregaard RO, Lovejoy TE, Kapos V, Santos AG, Hutchkings RW (1992) The biological dynamics of tropical rainforest fragments a prospective comparison of fragments and continuous forest. Bioscience 42:859–866

Borcard D, Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecol Model 153:51–68

Boscolo D, Tokumoto PM, Ferreira PA, Ribeiro JW, Santos JS (2017) Positive responses of flower visiting bees to landscape heterogeneity depend on functional connectivity levels. Perspect Ecol Conserv 15:18–24

Brehm G, Pitkin LM, Hilt N, Fiedler K (2005) Montane Andean rain forests are a global diversity hotspot of geometrid moths. J Biogeogr 32:1621–1627

Buddle CM, Langor DW, Pohl GR, Spence JR (2006) Arthropod responses to harvesting and wildfire: implications for emulation of natural disturbance in forest management. Biol Conserv 128:346–357

Colwell RK (2013) Estimates: statistical estimation of species richness and shared species from samples. Version 9. http://purl.oclc.org/estimates. Accessed 10 May 2018

Colwell RK, Chao A, Gotelli NJ, Lin SY, Mao CX, Chazdon RL, Longino JT (2012) Models and estimators linking individual-based and sample-based rarefaction, extrapolation, and comparison of assemblages. J Plant Ecol 5:3–21

Connell ML (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310

Costa FC, Pessoa KKT, Liberal CN, Filgueiras BKC, Salomão RP, Iannuzzi L (2013) What is the importance of open habitat in a predominantly closed forestarea to the dung beetle (Coleoptera, Scarabaeinae) assemblage? Rev Bras Entomol 57:329–334

Cuevas-Reyes P, Quesada M, Hanson P, Dirzo R, Oyama K (2004) Diversity of gall-inducing insects in a Mexican tropical dry forest: the importance of plant species richness, life-forms, host plant age and plant density. J Ecol 92:707–716

Didham RK, Hawton JH, Hammond PM, Eggleton P (1998a) Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. Philos Trans R Soc Lond B 353:437–451

Didham RK, Hammond PM, Lawton JH, Eggleton P, Stork NE (1998b) Beetle species responses to tropical forest fragmentation. Ecol Monogr 68:295–323

Downie NM, Arnett RH (1995) The beetles of northeastern North America: volume 1: introduction; suborders Archostemata, Adephaga, and Polyphaga, thru superfamily Cantharoidea. Sandhill Crane Press, Gainesvile

Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol Model 196:483–493

Ezcurra E (2016) Anthropogenic disturbances infiltrate forest fragments. Proc Natl Acad Sci USA 19:5150–5152

Fagundes C, Di Mare R, Wink C, Manfio D (2011) Diversity of the families of Coleoptera captured with pitfall traps in five different environments in Santa Maria, RS, Brazil. Braz J Biol 71:381–390

Filgueiras BKC, Liberal CN, Aguiar CDM, Hernández MIM, Iannuzzi L (2009) Attractivity of omnivore, carnivore and herbivore mammalian dung to Scarabaeinae (Coleoptera, Scarabaeidae) in a tropical Atlantic rainforest remnant. Rev Bras Entomol 53:422–427

Filgueiras BKC, Iannuzzi L, Leal IR (2011) Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest. Biol Conserv 144:362–369

Fleury M, Galetti M (2006) Forest fragment size and microhabitat effects on palm seed predation. Biol Conserv 131:1–13

Frazer GW, Canham CD, Lertzma KP (1999) Gap light analyzer (GLA), version 2.0: imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, user's manual and program documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York

Grimbacher PS, Cattedrall CP (2007) How much do site age, habitat structure and spatial isolation influence the restoration of rainforest beetle species assemblages? Biol Conserv 135:107–118

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD et al (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1:1–9

Halffter G, Favila ME (1993) The Scarabaeinae (Insecta: Coleoptera) an animal group for analyzing, inventorying and monitoring biodiversity in tropical rainforest and modified landscapes. Biol Int 27:15–21

Harper KA, Macdonald SE, Burton PJ, Chen J, Brosofske KD, Saunders SC, Euskirchen ES, Roberts D, Jaiteh MS, Esseen P (2005) Edge influence on forest structure and composition in fragmented landscapes. Conserv Biol 19:768–782

Hernández MIM, Barreto PSCS, Costa VH, Creão-Duarte J, Favila ME (2014) Response of a dung beetle assemblage along a reforestation gradient in *Restinga* forest. J Insect Conserv 18:539–546

Herrmann BC, Rodrigues E, Lima A (2005) A paisagem como condicionador de fragmentos florestais. Floresta 35:13–22

Hill MO (1973) Diversity and evenness: a unifying notation and its consequences. Ecology 54:427–431

Hill JK, Gray MA, Khen CV, Benedick S, Tawatao N, Hamer KC (2011) Ecological impacts of tropical forest fragmentation: how consistent are patterns in species richness and nestedness? Phil Trans R Soc B 366:3265–3276

Hillebrand H, Bennet DM, Cadotte MW (2008) Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. Ecology 89:1510–1520

Hooper DU, Chapin FS III, Ewell JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setala H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35

Hothorn T, Zeileis A, Farebrother RW, Cummins C, Millo G, Mitchell D (2018) Package “lmtest”. https://cran.r-project.org/web/packages/lmtest/lmtest.pdf. Accessed 25 Oct 2018

Iannuzzi L, Salomão RP, Costa FC, Liberal CN (2016) Environmental patterns and daily activity of dung beetles (Coleoptera: Scarabaeidae) in the Atlantic rainforest of Brazil. Entomotropica 31:196–207

Jost L (2006) Entropy and diversity. Oikos 113:363–375

Karen M, John O, John B, Paul G, Josephine P, Thomas K (2008) Distribution and composition of carabid beetle (Coleoptera, Carabidae) communities across the plantation forest cycle—implications for management. For Ecol Manag 256:624–632

Kutner M, Nachtsheim CJ, Neter J, Li W (2005) Applied linear statistical models. McGraw-Hill, New York

Larsen TH, Lopera A, Forsyth A (2006) Extreme trophic and habitat specialization by Peruvian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). Coleopt Bull 60:315–324

Lassau SA, Hochuli DF, Cassis G, Reid CAM (2005) Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? Divers Distrib 11:73–82

Leal IR, Filgueiras BKC, Gomes JP, Lannuzzi L, Andersen AN (2012) Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest. Biodivers Conserv 21:1687–1701

Legendre P, Legendre LFJ (1998) Numerical ecology. Elsevier, New York

Leps J, Smilauer P (2003) Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge

Lira AFA, Rego FNAA, Albuquerque CMR (2015) How important are environmental factors for the population structure of co-occurring scorpion species in a tropical forest? Can J Zool 93:15–19

Losey JE, Vaughan M (2010) The economic value of ecological services provided by insects. Bioscience 56:311–323

Luz RA, Fontes LS, Cardoso SRS, Lima EFB (2013) Diversity of the Arthropod edaphic fauna in preserved and managed with pasture areas in Teresina-Piauí-Brazil. Braz J Biol 73:483–489

Magnago LFS, Rocha MFR, Meyer L, Martins SV, Meira-Neto JAA (2015) Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic forest fragments. Biodivers Conserv 24:2305–2318

Magura T, Tóthmérész B, Elek Z (2004) Effects of leaf-litter addition on Carabid beetles in a non-native Norway spruce plantation. Acta Zool Acad Sci Hung 50:9–23

Maleque MA, Maeto K, Ishii HT (2009) Arthropods as bioindicators of sustainable forest management, with a focus on plantation forests. Appl Entomol Zool 44:1–11

Marcon E, Hérault B (2015) Measurement and partitioning of diversity, based on Tsallis entropy, following Marcon and Herault. https://cran.r-project.org/web/packages/entropart/entropart.pdf. Accessed 10 July 2018

McCune BP, Grace JB (2002) Analysis of ecological communities. MJM Software Design, Gleneden Beach

McIntyre NE (2000) Ecology of urban arthropods: a review and a call to action. Ann Entomol Soc Am 93:825–835

Moeed A, Meads MJ (1985) Seasonality of pitfall trapped invertebrates in three types of native forest, Orongorongo Valley, New Zealand. N Z J Zool 12:17–53

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nichols E, Larsen T, Spector S, Davis AL, Escobar F, Favila M, Vulinec K (2007) Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. Biol Conserv 137:1–19

Noss RF (1990) Indicators for monitoring biodiversity: a hierarchical approach. Conserv Biol 4:355–364

Noss RF (1999) Assessing and monitoring forest biodiversity: a suggested framework and indicators. For Ecol Manag 115:135–146

Novotny V, Basset Y (2000) Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. Oikos 89:564–572

Novotny V, Drozd P, Miller SE, Kulfan M, Janda M, Basset Y, Weiblen GD (2006) Why are there so many species of herbivorous insects in tropical rainforests? Science 313:1115–1118

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O’Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2018) Vegan: community ecology package. R package version 2.0-0. http://CRAN.R-project.org/package=vegan. Accessed 30 Oct 2018

Pearson DL, Cassola F (1992) World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. Conserv Biol 6:376–391

Prance GT (1987) Biogeography of neotropical plants. In: Whitmore TC, Prance GT (eds) Biogeography and quaternary history in tropical America. Oxford University Press, Oxford, pp 174–196

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rafael JA, Melo GAR, Carvalho CJB, Casari SA, Constantino R (2012) Insetos do Brasil, Diversidade e Taxonomia. Holos, Ribeirão Preto

Rainio J, Niemelä J (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. Biodivers Conserv 12:487–506

Ranta P, Blom T, Niemelä J, Joensuu E, Siitonen M (1998) The fragmented Atlantic rain forest of Brazil: size, shape and distribution of forest fragments. Biodivers Conserv 7:385–403

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

Rimbach R, Link A, Heistermann M, Gómez-Posada C, Galvis N, Heymann EW (2013) Effects of logging, hunting, and forest fragment size on physiological stress levels of two sympatric ateline primates in Colombia. Conserv Physiol 1:1–11

Rocha-Ortega M, Favila ME (2013) The recovery of ground ant diversity in secondary Lacandon tropical forests. J Insect Conserv 17:1161–1167

Rodríguez JP, Pearson DL, Barrera RR (1998) A test for the adequacy of bioindicator taxa: are tiger beetles (Coleoptera: Cicindelidae) appropriate indicators for monitoring the degradation of tropical forests in Venezuela? Biol Conserv 83:69–76

Salomao RP, Pordeus LM, Lira AFA, Iannuzzi L (2018) Edaphic beetle (Insecta: Coleoptera) diversity over a forest-matrix gradient in a tropical rainforest. J Insect Conserv 22:511–519

Salomão RP, Iannuzzi L (2015) Dung beetle (Coleoptera, Scarabaeidae) assemblage of a highly fragmented landscape of Atlantic forest: from small to the largest fragments of northeastern Brazilian region. Rev Bras Entomol 59:126–131

Santos BA, Peres CA, Oliveira MA, Grillo A, Alves-Costa CP, Tabarelli M (2008) Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. Biol Conserv 141:249–260

Sarges R, Halffter G, Díaz-Rojas A (2012) The importance of frugivory to the survival of the dung beetle *Onthophagus rhinolophus* Harold (Coleoptera: Scarabaeidae: Scarabaeinae) under changing ecological conditions. Coleopt Bull 66:166–168

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. Conserv Biol 5:18–32

Sayad E, Hosseini SM, Hosseini V, Salehe-Shooshtari MH (2012) Soil macrofauna in relation to soil and leaf litter properties in tree plantations. J For Sci 58:170–180

Sayer EJ, Sutcliffe LME, Ross RIC, Tanner EVJ (2010) Arthropod abundance and diversity in a lowland tropical forest floor in Panama: The role of habitat space vs. nutrient concentrations. Biotropica 42:194–200

Silva JMC, Casteleti CHM (2003) Status of the biodiversity of the Atlantic Forest of Brazil. In: Galindo-Leal C, Câmara IG (eds). The Atlantic Forest of South America: biodiversity status, threats and outlook. Island Press and CABS, Washington, DC, pp 43–59

Silva RKS, Feliciano ALP, Marangon LC, Lima RBA (2010) Floristics and ecological succession of the arboreal vegetation in the spring are of an Atlantic forest fragment, Pernambuco, Brazil. Rev Bras Cienc Agrárias 5:550–559

Stem C, Margoluis R, Salafsky N, Brown M (2005) Monitoring and evaluation in conservation: a review of trends and approaches. Conserv Biol 19:295–309

Tabarelli M, Peres CA, Melo FPL (2012) The 'few winners and many losers' paradigm revisited: Emerging prospects for tropical forest biodiversity. Biol Conserv 155:136–140

Tanaka LK, Tanaka SK (1982) Rainfall and seasonal changes in arthropod abundance on a tropical oceanic island. Biotropica 14:114–123

ter Braak CJF, Šmilauer P (2003) CANOCO reference manual and CanoDraw for windows user's guide: software for canonical community ordination. Biometris, Wagenigen

Turner IM (1996) Species loss in fragments of tropical rain forest: a review of the evidence. J Appl Ecol 33:200–209

Valois MC, Vaz-de-Mello FZ, Silva FAB (2017) Taxonomic revision of the Dichotomius sericeus (Harold, 1867) species group (Coleoptera: Scarabaeidae: Scarabaeinae). Zootaxa 4277:503–530

Vanderwall MC, Malcolm JR, Smith SM, Islam N (2006) Insect community composition and trophic guild structure in decaying logs from eastern Canadian pine-dominated forest. For Ecol Manag 15:190–199

Vasconcellos A, Andreazze R, Almeida AM, Araujo HFP, Oliveira ES, Oliveira U (2010) Seasonality of insects in the semi-arid Caatinga of northeastern Brazil. Rev Bras Entomol 54:471–476

Wardhaugh CW, Edwards W, Stork NE (2013) Variation in beetle community structure across five microhabitats in Australian tropical rainforest trees. Insect Conserv Divers 6:463–472

Wiezik M, Svitok M, Dovciak M (2007) Conifer introductions decrease richness and alter composition of litter-dwelling beetles (Coleoptera) in Carpathian oak forests. For Ecol Manag 247:61–71

Wilson EO (1988) Biodiversity. The National Academies Press, Washington, DC

Wolda H (1978) Seasonal fluctuations in rainfall, food and abundance of tropical insects. J Anim Ecol 47:369–381

Wolda H (1989) Seasonal cues in tropical organisms. Rainfall? Not necessarily! Oecologia 80:437–442

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York