



Original Articles

Cross-taxon congruence in insect responses to fragmentation of Brazilian Atlantic forest



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ABSTRACT

Anthropogenic disturbance causes many impacts across multiple levels of biological organization from populations to ecosystems. However, the extent of cross-taxon congruence in biotic responses to disturbance, and therefore the utility of using particular taxa as indicators of broader biotic responses, is poorly known. In this study, we examine the extent to which variation in alpha diversity, beta diversity and species composition of ants, fruit-feeding butterflies, dung beetles and termites in relation to fragment size are congruent in the highly fragmented Brazilian Atlantic forest. Our results show generally low and inconsistent congruence, typically occurring for particular pairs of taxa only (such as butterflies and dung beetles for species composition, and ants and termites for Hill diversity-¹D) or not at all (such as for species richness). In synthesis, there some universal community-level attributes and taxa (i.e., attributes responding consistently and congruently across taxa) have been proved to be sensitive in general. Vegetation structure and spatial location of fragments were not significant predictors of ant and termite species composition, but explained 21% and 40% of the variation in species composition of dung beetles and butterflies, respectively. In addition, we found no general increase in the ratio of generalists to specialists with decreasing fragment size. The overall lack of cross-taxon congruence means that a single taxon cannot provide a reliable indication of biotic responses to fragmentation in our study system. This can be explained by taxon-specific responses to variation in tree diversity, tree functional attributes and the spatial location of fragments. Our study therefore provides support for a multi-taxon approach to biodiversity monitoring and conservation planning.

1. Introduction

Burgeoning human populations have driven deforestation throughout the tropics, often transforming old-growth forests into small and isolated fragments surrounded by an inhospitable matrix (Tabarelli et al., 2010). Such remaining vegetation is exposed to a wide range of biodiversity-threatening processes related to both direct and indirect effects of habitat loss and fragmentation (Fahrig, 2003). These threats operate both within fragments (e.g. edge effects, and disturbances such as logging and fire) and at the landscape scale (e.g. isolation effects), with severe but frequently contrasting impacts on species with high conservation and functional value (Barlow et al., 2016).

Forest biodiversity generally declines along a gradient from old-growth forest through agroforestry, secondary forest stands and small

forest remnants or edge-affected habitats, plantations, pastures and intensive agriculture (Barlow et al., 2007; Gardner et al., 2008; Solar et al. 2016). Accordingly, assemblages are impoverished both taxonomically and functionally in non-forest and edge-affected habitats due to the replacement of specialist, disturbance-sensitive species by a small set of generalist or disturbance-adapted species, eventually leading to biotic homogenization at the landscape level (Olden et al., 2004; Clavel et al., 2011; Tabarelli et al., 2012). Specialists and other sensitive groups therefore tend to be described as disturbance ‘losers’ and generalists as disturbance ‘winners’ (*sensu* Tabarelli et al., 2012).

Despite the numerous studies on biotic responses to habitat loss and fragmentation, the extent to which different taxa exhibit consistent changes in species richness and composition remains poorly examined. Such cross-taxon congruence has important implications both for

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ecological theory in terms of understanding the drivers of fragmentation impacts, and for conservation practice in relation to the use of particular taxa as indicators of broader ecological responses.

Insects are the dominant group of invertebrates in most terrestrial ecosystems, both taxonomically and functionally (Aizen and Feinsinger, 1994; Didham et al., 1996; Wirth et al., 2008). Along with their sensitivity to environmental changes, this makes some insect groups ideal bio-indicators of ecological change (e.g., McGeoch, 1998; Andersen and Majer, 2004; Uehara-Prado et al., 2009; Andrade et al., 2014; Luke et al., 2014). However, if different taxa show idiosyncratic responses, single-taxon studies will have limited relevance to biodiversity monitoring and conservation planning (Hayes et al., 2009; Leal et al., 2010). The adoption of a ‘shopping basket’ approach involving multiple taxa with contrasting ecological roles and habitat specializations has therefore been advocated for effectively documenting broader biodiversity responses (Kremen et al., 1993; Basset et al., 2008; Andrade et al., 2014; Hevia et al., 2016). The use of multiple taxa can also provide more comprehensive information on both functional and phylogenetic responses (Leal et al., 2012; Carrié et al., 2017).

Here we examine cross-taxon congruence in insect responses to fragmentation in Atlantic forest of north-eastern Brazil. This region has experienced intense habitat loss and fragmentation, with nearly 90% of its original extent already cleared or substantially modified (Silva and Casteleti, 2003; Ribeiro et al., 2009). Many studies have described fragmentation-related effects on particular faunal taxa (Oliveira et al., 2004; Uehara-Prado et al., 2007; Filgueiras et al., 2011; Leal et al., 2012). These effects are often related to fragmentation-related variation in vegetation structure and tree species richness (see Santos et al., 2008; Lopes et al., 2009), which have cascading effects on higher trophic levels, including insects (Lopes et al., 2009; Leal et al., 2014). Fragmentation of Atlantic Forest also often results in extensive winner (generalists)-loser (specialists) replacements of tree species across multiple spatial scales (Lôbo et al., 2011), leading to taxonomic and functional impoverishment in edge-affected habitats (see Santos et al., 2008; Tabarelli et al., 2008).

Our study uses previously published data on ants, fruit-feeding butterflies, dung beetles and termites collected at the same set of forest fragments. Our first aim is to evaluate the extent of cross-taxon congruence in terms of variation in species diversity (both alpha and beta) and composition along a gradient of fragment size. Variation in alpha diversity has direct implications for the use of insects as biodiversity indicators (*sensu* McGeoch, 1998), knowledge of beta diversity is important for understanding species turnover across forest fragments of different size (Ribeiro et al., 2008; Filgueiras et al., 2016a), and variation in species composition relates directly to the use of particular insect groups as indicators of broader ecological change. We include an analysis of compositional responses of the different taxa to tree diversity, tree functional attributes and fragment location, to explain the extent of cross-taxon congruence. Our second aim is to examine the consistency of specialist-generalist replacements in fragmented habitats. We address the question: to what extent does the generalist/specialist (G/S) ratio in terms of both abundance and species richness consistently increase with decreasing fragment size?

2. Materials and methods

2.1. Study sites

The study was conducted in the Usina Serra Grande (Fig. A1), a large (667 km²) sugar-cane estate in northeastern Brazil (8°30'S, 35°52'W). This landscape contains nearly 100 forest fragments (range in size: 1.67–3500 ha), including the Coimbra forest – the largest (3500 ha) and best-preserved fragment of Atlantic forest in north-eastern Brazil (Grillo et al., 2006). Our study involved 19 forest fragments (Table A1), nine of which were classified as small (< 50 ha), six as medium (≥ 50 and < 100 ha) and four as large (≥ 100 ha; including

the Coimbra forest) (*sensu* Pardini et al., 2005) (Table A1). To minimize the influence of isolation, fragments covered (%) approximately the same range of distance to the next fragment (see Table A1). All remnants are embedded in old matrix of sugar-cane fields. The edges of remnants (< 100 m from the forest border) are dominated by pioneer tree species, with impoverished sets of shade-tolerant, vertebrate pollinated, and large-seeded vertebrate dispersed tree species (Oliveira et al., 2004; Melo et al., 2006; Lopes et al., 2009).

2.2. Insect surveys

Ants were extracted from 30 1-m² leaf litter samples collected at 10 m intervals along a 300-m transect running through each site, between September 2007 and March 2008 (see Leal et al., 2012, for details). Sampling of dung beetles was carried out using a combination of pitfall traps and flight intercept traps, between September 2007 and March 2008 (see Filgueiras et al., 2011, for details). Ten sets of four pitfall traps (one unbaited, and the others baited with human faeces, fermented banana, and decomposing bovine spleen respectively) each set spaced 20 m apart were established at each of the transects used to sample ants, and operated for 48 hrs (Filgueiras et al., 2011). Termite surveys were conducted in the same permanent transects as ants and dung beetles specifically in forest interior areas, between October 2008 and April 2009. A rapid sampling protocol of termite biodiversity was applied in each fragment, involving comprehensive surveys of 15 5 m × 2 m quadrats, taking one person/hr per quadrat (see Oliveira et al., 2013, for details). Fruit-feeding butterflies were sampled (hereafter butterflies) using bait traps at nine of the 19 fragments (Fig. A1), between November 2012 and January 2013. In each site, five traps were arranged linearly with 30 m spacing in forest interior areas, and operated for four consecutive days from November 2012 to January 2013 (see Filgueiras et al., 2016b for details). For more details about sample processing please see Filgueiras et al., 2011, Leal et al., 2012, Oliveira et al., 2013, and Filgueiras et al., 2016b.

2.3. Tree attributes and the spatial location of fragments

All trees with a diameter at breast height > 10 cm were surveyed across a network of 0.1-ha plots, in which insect communities had been previously surveyed. Tree species were further assigned into ecological groups regard to regeneration strategy (pioneer, and shade-tolerant trees), forest vertical stratification (understory, canopy and emergent trees) and fruit size (small < 15 mm, large > 15 mm), as detailed in Table A1. We use the spatial location of fragments regarding their coordinates using UTM projections (SAD 69 DATUM). In fragmented landscapes, the spatial location of forest fragments can be an important driver in shaping the distribution and abundance of tree species (Mendes et al., 2016), which in turn can affect insect communities.

2.4. Specialist-Generalist classification

Ants, dung beetles and termites were classified according to diet. Ants were classified as specialists or generalists based on a functional group scheme designed specifically for Atlantic forest, as described by Leal et al. (2012). Arboreal dominants, Army ants, Cryptic omnivores, Cryptic predators, Epigaeic predators and Non-leaf cutting Attini were classified as specialists, and Epigaeic omnivores, and Opportunists as generalists (Leal et al., 2012). Dung beetle species were classified as specialists if they were either coprophagous, saprophagous or necrophagous, defined by > 70% capture of individuals in traps baited with human faeces, fermented banana and bovine spleen respectively; all other species were classified as generalists (Filgueiras et al., 2011). Termites were also classified according to feeding groups: specialist wood-, soil- and leaf-feeders as specialists, and wood/soil interface-feeders and wood/leaf-feeders as generalists (Oliveira et al., 2013). As butterfly species in this study are frugivorous, we grouped butterfly

species into three categories of habitat preference: forest, edge and open habitat, following Brown, 1992; Koh et al., 2004; Uehara-Prado et al., 2007; Sant'Anna et al., 2014. We classified forest-dependent species as specialists, and edge and open-habitat species as generalists. In general, Atlantic forest butterfly species associated with open or/and edge-affected habitats show a generalist diet (Uehara-Prado et al., 2007).

2.5. Data analyses

2.5.1. Species diversity and composition

We used two measures of alpha-diversity: (i) species richness (i.e., the number of species sampled); and (ii) Hill diversity 1D , which weights each species according to its proportional abundance in the sample, and therefore reflects the number of common species (Jost, 2006). We assessed the compositional completeness of each habitat using EstimateS 9.1 (Colwell, 2013) by calculating the number of species observed as a percentage of the total estimated richness (i.e., sampling completeness) based on non-parametric estimators (Bootstrap, Chao 2, Jack 1 and Jack 2, see Colwell, 2013). We used Spearman rank correlations (due to the absence of normality or homoscedasticity in some variables) to test for correlations among taxa in alpha-diversity (1D , species richness) and the Mantel tests for cross-taxon correlations among functional group composition (correlating the similarity matrices of Bray-Curtis index). We used Bray-Curtis similarity because it has many properties amenable to ecological data, including independence from scale of measurement and from joint absences (Clarke and Warwick, 1994).

We analysed variation in beta-diversity among insect groups using the multivariate homogeneity of group dispersions, to calculate the average distance of group members to the group centroid (spatial median) in multivariate space (Anderson, 2006) for each insect group. We examined variation in species composition using nonmetric multidimensional scaling (NMDS) with Bray-Curtis as the measure of dissimilarity to represent the fragment-size groups and distances to centroids on the first two PCoA axes. Non-euclidean distances between objects and group centroids are handled by reducing the original distances to principal coordinates (Anderson, 2006).

2.5.2. Tree and spatial attributes

We adopted a two-step approach to assessing the importance of tree attributes and the spatial location of fragments as environmental drivers of variation in species composition of the different insect taxa. First, we performed a Principal Components Analysis (PCA) using data on tree attributes to convert a set of observations of possibly correlated variables in terms of vegetation structure into a set of values of linearly uncorrelated variables. We then used Multiple Regressions on distance Matrices (MRM) to construct a set of candidate models using ant, butterfly, dung beetle and termite species composition as response variables and vegetation structure and the spatial location of fragments as predictor variables. For this, we calculated a geographic distance matrix (Euclidean) between forest fragments based on their geographic coordinates (the spatial location) and other distance matrix (Euclidean) based on PCA (axes 1 and 2) showing the variation in terms of vegetation structure among forest fragments. All these analyses were carried out using R 3.2.4 (R Development Core Team, 2015).

2.5.3. Generalist/specialist replacement

For each insect group, variation among fragment classes in G/S ratios in terms of both abundance and species richness were analyzed by one-way ANOVA and subsequent Tukey post hoc tests for pair-wise comparisons.

Table 1

Species richness and sample completeness of ants, butterflies, dung beetles and termites sampled in Atlantic forest, Alagoas, northeastern Brazil.

Taxon	α	α_{est} (mean \pm SE) ^a	Completeness (%) ^b	Coverage (%) ^c
Ants	146	167.03 (5.37)	87	53
Butterflies	57	70.48 (2.92)	81	21
Dung beetles	30	43.32 (3.88)	69	11
Termites	40	44.37 (1.17)	90	15

^a Estimated species richness based on the average of four abundance-based richness estimators, Bootstrap, Chao 2, Jack 1 and Jack 2 (see Colwell 2013).

^b Number of species observed as a percentage of the total estimated richness.

^c Number of species observed as a percentage of the landscape total.

3. Results

3.1. Alpha diversity and cross-taxon congruence

Ants were the most diverse group at both local and regional scales, with a total of 146 species recorded and mean site richness (\pm SE) of 53 ± 2.09 species. The least diverse group was dung beetles, with 30 species and mean site richness (\pm SE) of 5.9 ± 0.66 species (see Table 1). Sampling completeness (number of species observed as a percentage of the total estimated richness) based on non-parametric estimators (Bootstrap, Chao 2, Jack 1 and Jack 2, see Colwell, 2013) was 70% for dung beetles, 81% for butterflies, 87% for ants, and 90% for termites (Table 1).

There was an extremely high correlation between ants and termites for 1D ($r = 0.96$; $p = 0.001$), and species richness was also significantly correlated for these taxa ($r = 0.45$; $p = 0.04$). However, there were no significant correlations for either species richness or 1D for any other pair of insect groups (Table 2). Similarity matrices based on species and functional group composition were significantly correlated within ants and dung beetles (Table A2), but cross-taxon correlations were significant only when regarding ants and termites (Table A2).

3.2. Beta diversity

The average distance-to-centroid value ranged from 0.424 for termites to 0.614 for ants, and varied significantly among insect groups (ANOVA $F = 9.81$, $df = 3$, $P < 0.001$) (Fig. 1). The results of pairwise comparisons show significant differences in beta diversity between dung beetles and termites ($p < 0.001$), butterflies and termites ($p < 0.001$) and ants and termites ($p < 0.001$) (see Fig. 1).

There were no significant differences in multivariate dispersion among fragment classes for any insect group, although small fragments show higher beta diversity than large fragments for ants, dung beetles and termites (Fig. 2).

3.3. Relationships with fragmentation metrics and vegetation structure

The first axis of PCA based on vegetation structure explained 63.5% of the total variation of vegetation structure among fragments, and it was associated with shade-tolerant trees, pioneer trees and trees with

Table 2

Results of pairwise Spearman's correlations values of species richness (above the diagonal) and Hill diversity (1D , below) among the four insect groups in Atlantic forest fragments at Usina Serra Grande, Alagoas, north-eastern Brazil.

Taxon	Ants	Butterflies	Dung beetles	Termites
Ants	–	0.07	0.24	0.45 [*]
Butterflies	0.32	–	0.31	0.16
Dung beetles	0.51	0.23	–	0.15
Termites	0.96 [*]	0.11	0.10	–

^{*} $P < 0.05$.

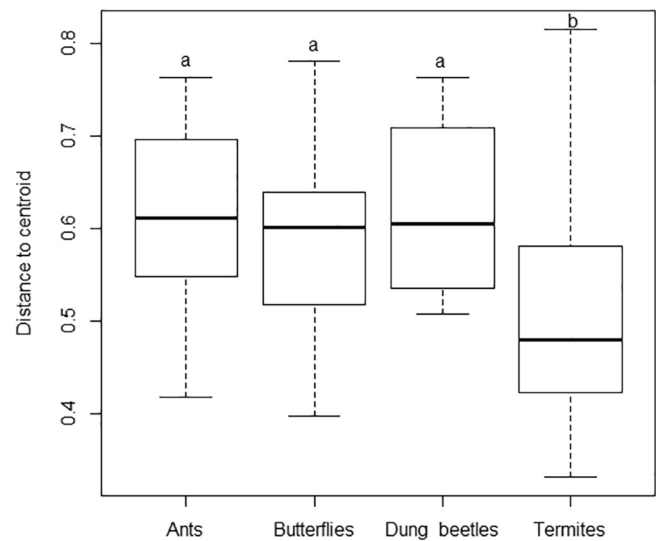


Fig. 1. Distanced to centroid (a measure of beta-diversity) of each insect group in Atlantic forest fragments at Usina Serra Grande, Alagoas, north-eastern Brazil.

Table 3
Summary statistics for predictor variables (vegetation structure-PCA Axes and the spatial location of fragments) from Multiple Regressions on distance Matrices (MRM) showing only significant models. Response variables included ants, butterflies, dung beetles and termite species composition regarding the entire community and separately in terms of generalist and specialist species.

Predictor variable	Coefficient	P
Butterflies ~ PCA + Spatial Location	$R^2 = 0.09$	
PCA	40.61	0.02*
Spatial Location	3.91	0.79
Dung beetles ~ PCA + Spatial Location	$R^2 = 0.18$	
PCA	14.81	0.1
Spatial Location	21.11	0.01*
Dung beetles Generalists ~ PCA + Spatial Location	$R^2 = 0.19$	
PCA	5.78	0.04*
Spatial Location	4.61	0.21

* $P < 0.05$.

large (> 15 mm) and small fruits (< 15 mm) (Table A3). The second axis explained 20.4% of the total variation and was associated with tree density (see Table A3).

According to our MRM models, the four insect taxa varied markedly in terms of their relationships with vegetation structure and spatial location of fragments. These explanatory variables were not significant predictors of ant and termite species composition, but explained 21% and 40% of the variation in species composition of dung beetles and

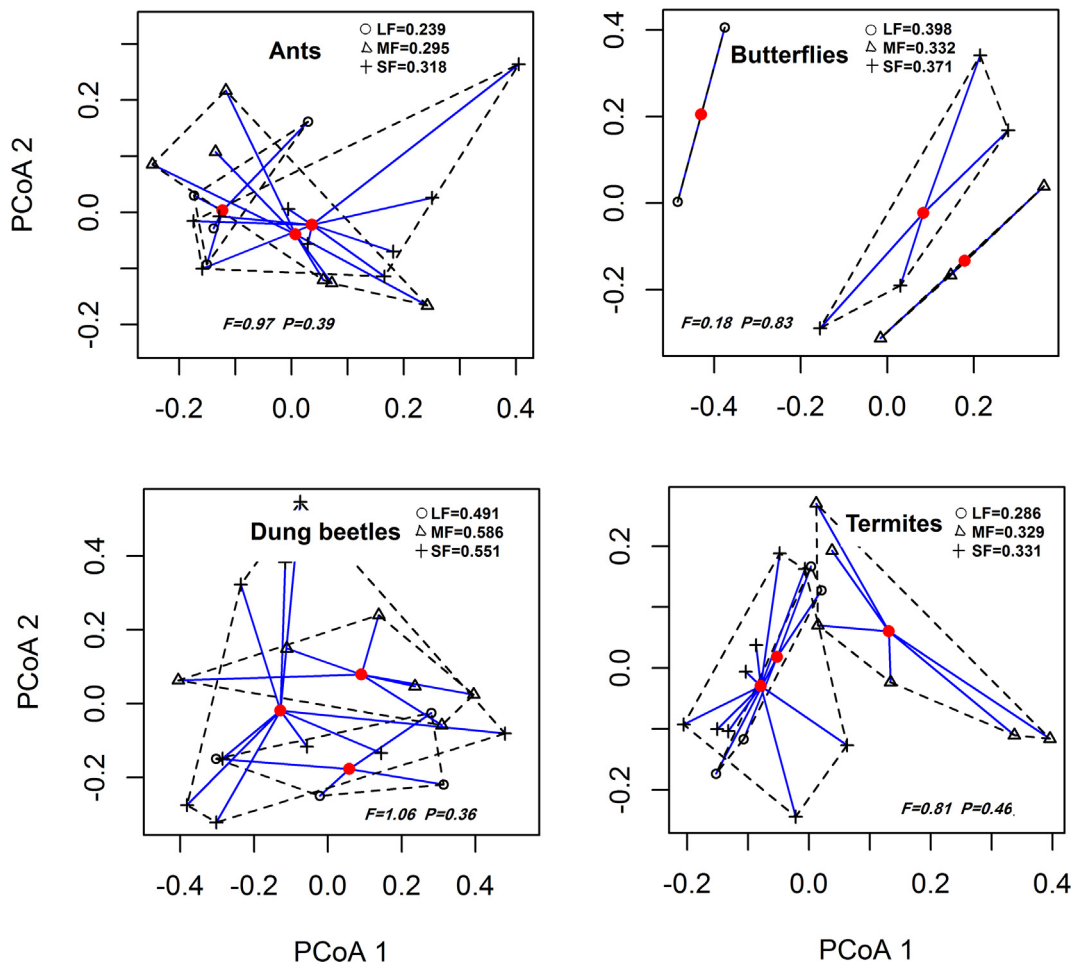


Fig. 2. Nonmetric multidimensional scaling (NMDS) plots on the first two PCoA axes of each insect group among fragment classes (SF-small fragments < 50 ha, MF-medium-sized fragments 50–100 ha and LF-large fragments > 100 ha) at Usina Serra Grande, Alagoas, north-eastern Brazil. The symbols represent the variation shown by each fragment class, and red dots are the locations of the group centroids on the principal coordinates.

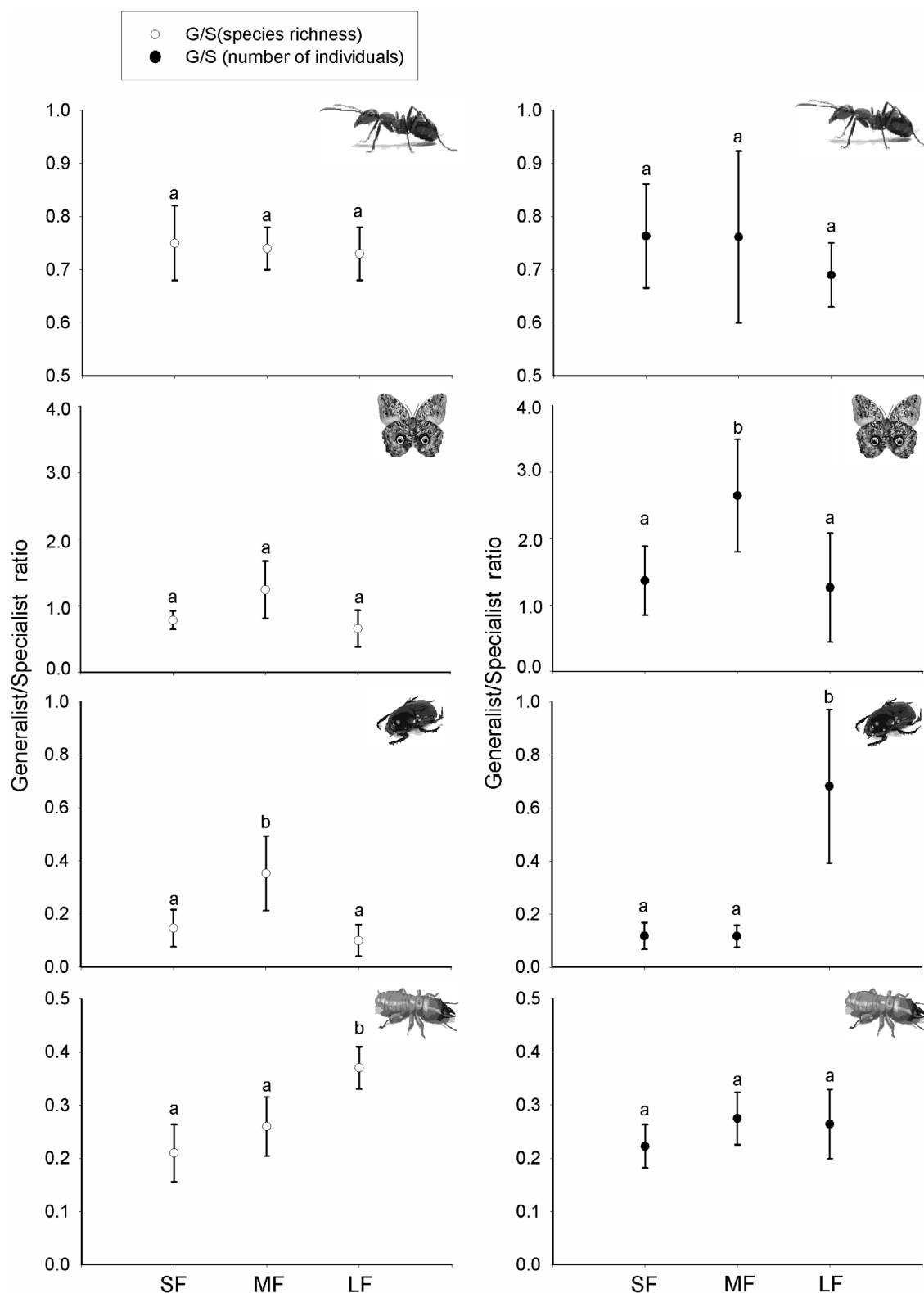


Fig. 3. Generalists/Specialists (Mean \pm SE) ratio of species richness (white circles) and number of individuals (black circles) per plot across small (SF; < 50 ha), medium-sized (MF; 50–100 ha) and large fragments (LF; > 100 ha) at Usina Serra Grande, Alagoas, north-eastern Brazil. The values followed by the same letters are not significantly different according to Tukey test.

butterflies respectively (Table 3).

3.4. Generalist/Specialist ratio

In most cases the ratio of generalist to specialist species and

individuals was not significantly different in large compared with small fragments, and in the two cases of significant difference (dung beetle abundance and termite richness) the ratio was higher rather than lower in large fragments (Fig. 3). More specifically, our results showed that there was evidence of replacement of specialist species by generalists

with declining fragment size for dung beetles with an opposite pattern for termites (Fig. 3).

4. Discussion

4.1. Community-level attributes and cross-taxon congruence

A multi-taxa approach can help to understand the effects of disturbances on biodiversity persistence across human-modified landscapes regarding idiosyncratic responses of different ecological groups (Andrade et al., 2014). Here we examine whether there is cross-taxon congruence in insect responses to fragmentation-related effects in a hyper-fragmented landscape of the Brazilian Atlantic forest regarding different community-level attributes. Our results indicate that particular pairs of taxa tend to respond both consistently and congruently in terms of particular attributes such as species diversity (ants and termites), functional ratio (dung beetles and termites) and taxonomic composition (butterflies and dung beetles), while all taxa do not exhibit either consistent (i.e. trend related to explanatory variables) or congruent response in terms of alpha and beta diversity. In general, there was low cross-taxon congruence in terms of alpha diversity among fragments with only ants and termites species exhibiting significant correlations. Moreover, the four taxonomic groups showed inconsistent responses in terms of beta-diversity. This can be explained by inconsistent responses to variation in tree functional attributes and the spatial location of fragments. Finally, there was evidence of replacement of specialist species by generalists with declining fragment size for dung beetles with an opposite pattern for termites.

Our study shows the cross-taxon congruence between ants and termites in terms of alpha diversity. This can be associated with the potential interaction between them, which many ants feed on termites as well as mutualistic interaction (Dejean and Fénelon, 1999; Diehl et al., 2005). In addition, these insects may interact indirectly through changes they make to their environments, with both affecting soil properties and resource availability by their nest building and feeding (Luke et al., 2014). However, the lack of cross-taxon congruence among insect groups as well as the heterogeneity in terms of beta diversity values reinforces that notion that effects of land-use transformation on biodiversity differed significantly among the various biotic groups (Hevia et al., 2006). Following this idea, it is not a surprise that the cross-taxon congruence in terms of some community-level attributes, such as species richness was low given that the taxa are so ecologically different. This low congruence in terms of species richness was consistent with other cross-taxon tropical studies. Barlow et al. (2007) examining the conservation value of tropical primary, secondary, and plantation forests for 15 taxonomic groups in Amazonia forest found a very weak cross-taxon congruence in response patterns to land-use when evaluated species richness data. Andrade et al. (2014) to compare species richness of ants, birds, dung beetles and plants in undisturbed forest and gradients of forest disturbed by forest fires showed no correlation between taxa. In Brazilian Atlantic forest, Uehara-Prado et al. (2009) to compare species richness of beetles (i.e. Carabidae, Scarabaeidae, Staphylinidae, and epigeic Coleoptera) between large fragments and disturbed forest areas found that this response variable was not significantly correlated between any pair of taxa. According to these studies, this absence or weak cross-taxon congruence is associated with idiosyncratic responses to land-use changes.

Moreover, our results highlight that this lack of congruence can be explained by the inconsistent insect responses to variation in explanatory variables. In Atlantic forest, the spatial location of fragments and vegetation structure appeared to be an important predictor of dung beetle and butterfly species composition, respectively. These different perceptions can be related with the fact that more specialised species as well as the generalists are distinct sensitive to disturbance-induced loss of key resources (Uehara-Prado et al., 2007; Leal et al., 2012). For instance, more specialized dung beetles are strongly driven by the

availability of vertebrate dung, which in turn are negatively affected by habitat loss and fragmentation (Estrada et al., 1999; Nichols et al., 2009), as well as habitat or landscape structure (e.g. spatial distribution of fragments) (Filgueiras et al., 2011). On the other hand, forest fragmentation often favours common, generalist species with these unspecialised species buffered a wide habitat tolerances, flexible nesting requirements and generalised diets (Andersen, 1995; Leal et al., 2012). This can help to explain the significantly response of fruit-feeding butterflies to changes in vegetation attributes (i.e. tree assemblages) across forest fragments, where butterflies more tolerant to sunlight and drought are more abundant (Uehara-Prado et al., 2007; Filgueiras et al., 2016b), while forest-dwelling butterfly species with more specialized diet are highly sensitive to fragmentation- and plant-related variables, such as forest cover and pioneer tree species (Filgueiras et al., 2016b).

Our results also show no significant variations of G/S ratios of ant species richness as well as contradictory response for other taxa (e.g. large fragments showing highest values of G/S ratios considering termite species richness). This absence or contradictory responses of some taxonomic groups to disturbance also can be associated with the compensatory dynamics (Supp and Ernest, 2014). Accordingly, the loss or decline of forest-dependent species (i.e. disturbance-sensitive species) may be compensated by the proliferation of disturbance-adapted species maintaining community-level attributes (e.g. abundance, species richness, phylogenetic diversity) across human-modified tropical landscapes (Russildi et al., 2016; Morante-Filho et al., 2017). Although multi-taxa response to habitat change reported a general trend of decreasing species richness (mainly rare and specialist species) with increasing habitat modification (Schulze et al., 2004), generalists (disturbance-adapted species) can proliferate across disturbed habitats (Russildi et al., 2016). In fact, habitat loss and fragmentation influence positively the richness of a range of generalist ant functional groups (e.g. opportunist ants) in Brazilian Atlantic forest, where these species are more flexible in terms of diet and nesting requirements than specialised ants (Leal et al., 2012). Additionally, termites are less consistent in terms of response in Atlantic forest fragments, where habitat loss and fragmentation no affect species richness and abundance of these insect groups (Oliveira et al., 2013). This resilience or resistance of termites to habitat change was also related in other tropical studies (Luke et al., 2014; Basset et al., 2017), where the magnitude of faunal changes between forest and disturbed habitats was less drastic for termites than for other insect groups.

4.2. Conclusions

In synthesis, our study has contributed to an improved understanding of multi-taxa patterns of species richness (alpha diversity), species turnover (beta diversity), as well as species composition among insect groups with different ecological roles in a hyper-fragmented landscape. As there are community-level attributes and taxa most sensitive to habitat change than others, our results support a multi-taxonomic approach with a high diversity of community-level attributes to biodiversity assessments and conservation planning in human-modified landscapes. On the other hand, the absence or contradictory response of these insect groups to explanatory variables can be an indicative of compensatory dynamics, which can be associated with the predominance of generalist species along Atlantic forest fragments converting unique regional biotas into a collection of low-diversity assemblages. As generalist species are not able to perform all functions and services provided by specialist groups (Kupfer and Franklin, 2009), the proliferation of disturbance-adapted species has a decisive role on biodiversity persistence in hyper-fragmented landscapes with a consequent reduction in ecosystem services (Leal et al., 2014). However, as the long-term trajectories of biodiversity in fragmented landscapes may differ (Ewers et al., 2017), further studies should examine biotic responses to disturbance across several ecological groups, including their ability to persist in human-modified landscapes as they continue to

move toward edge-dominated landscapes.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2018.11.036>.

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