BIODIVERSITY RESEARCH

Spatial replacement of dung beetles in edge-affected habitats: biotic homogenization or divergence in fragmented tropical forest landscapes?

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ABSTRACT

Aim In this study, we investigate whether anthropogenic land use and habitat fragmentation lead to a process of either homogenization (decreasing spatial replacement and increasing nestedness) or divergence (increasing spatial replacement and decreasing nestedness) of dung beetle assemblages in edge-affected habitats.

Location A fragmented landscape of the Atlantic forest of north-east Brazil.

Methods We investigate the extent to which beta diversity of dung beetle assemblages varies in edge-affected habitats at different spatial scales (i.e. traps along an interior–exterior nonlinear gradient, within and among habitats). We compare species replacement and nestedness of dung beetle assemblages using (1) multiple dissimilarity measures accounting for compositional heterogeneity across forest (i.e. forest edges, core primary forest areas and small fragments) and matrix habitats (i.e. sugar cane plantations and pastures) and (2) distance matrices accounting for the multivariate structure of dissimilarity.

Results (1) Each habitat supported a distinct dung beetle assemblage; (2) there was a strong influence of anthropogenic land use and fragmentation-related effects on dung beetle β-diversity, with species replacements increasing in edge-affected and matrix habitats providing support for the divergence hypothesis at all spatial scales; (3) edge effects enhanced species replacement across assemblages; (4) dung beetle assemblages were not randomly distributed, with habitat type leading to a strongly nested pattern of species composition; and (5) both dung beetle replacement and nestedness were not correlated with geographic distance, whereby neighbouring sites were not necessarily more similar in their community composition.

Main conclusions Species replacement is strongly influenced by habitat configuration and β-diversity increases in edge-affected habitats. Accordingly, anthropogenic land use and habitat fragmentation clearly promote community-level taxonomic divergence in human-modified landscapes. Landscape-scale divergence likely results from a non-random distribution of both forest-dependent and disturbance-adapted species across all habitats, which are in marked contrast in terms of suitability.

Keywords

Atlantic forest, edge effects, land use, nested pattern, Scarabaeinae, species turnover.

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INTRODUCTION

The long-term prospects for tropical forest biodiversity and ecosystem services are inextricably linked to the expansion of human-modified landscapes as they tend to support a myriad of small forest fragments embedded within a harsh, open-habitat matrix (Melo *et al.*, 2013). As agricultural frontiers are consolidated and old-growth forest patches become rare and more isolated, few highly resilient species 'winners' are expected to dominate ecological communities at the expense of forest-dependent species 'losers', which are unable to tolerate anthropogenic disturbances (Tabarelli *et al.*, 2012). This relentless substitution of 'losers' by 'winners' may lead to increased species similarity among two or more communities, with hyperdominant species contributing to reduced taxonomic β-diversity across multiple spatial scales (Lôbo *et al.*, 2011; Arroyo-Rodríguez *et al.*, 2013). Such a biotic homogenization (McKinney & Lockwood, 1999) may also result in reduced genetic, taxonomic and/or functional β-diversity (Olden *et al.*, 2004). This phenomenon can be analysed according to a nested-subset concept (Wright *et al.*, 1998), which predicts that the assemblages in low-diversity fragments will consist of a subset of those species inhabiting more pristine forest stands.

On the other hand, community divergence and increments in β-diversity can also emerge in fragmented tropical landscapes, particularly across communities inhabiting different landscapes (Laurance *et al.*, 2007). The 'landscape-divergence hypothesis' (*sensu* Laurance *et al.*, 2007) predicts that fragments within the same landscape tend to experience increasing taxonomic similarity, while fragments in different landscapes tend to diverge. Divergence is modulated by spatio-temporal variation in edge effects, the main force affecting community structure (at least in the case of sedentary organisms such as plants), which in turn reflects the environmental conditions exhibited by the matrix (Laurance *et al.*, 2007).

Dung beetle species are frequently adopted as indicators of either natural or anthropogenic disturbance in tropical forests (Spector, 2006; Nichols *et al.*, 2007; Gardner *et al.*, 2008; Braga *et al.*, 2013; Filgueiras *et al.*, 2015). However, there is no consensus on dung beetle responses to habitat disturbance. Sampling design limitations and uncontrolled biogeographic- and landscape-related biases often limit generalizations (Gardner *et al.*, 2008). Additionally, the spatial organization of dung beetle β-diversity has been rarely examined in human-modified landscapes, particularly the β-diversity responses to changes in landscape spatial configuration. Such frailties in the history of research design have probably contributed to overestimates of the conservation value of anthropogenic landscapes for dung beetle species (Gardner *et al.*, 2008).

The use of turnover metrics can help estimate the relative importance of changes in forest cover, landscape configuration and habitat quality as predictors of spatial patterns of variation in dung beetle assemblages in human-modified landscapes. Moreover, analyses of species replacement and nestedness among sites, and in particular their relative importance at different spatial scales, can provide key insights into the processes driving both local and regional patterns of species diversity (Rouquette *et al.*, 2013). Understanding patterns of species replacement and nestedness can therefore have important implications for conservation. For instance, communities with high degrees of nestedness in a landscape would require the prioritization of a few high-diversity habitats in conservation planning, whereas those with high spatial turnover would benefit from a regional approach focused on protecting multiple habitats (Wright & Reeves, 1992). These priority-setting approaches are relevant in fragmented landscapes, where habitat loss and resulting increases in edge-affected areas and edge-to-interior ratios have a pervasive impact on biodiversity (Ewers & Didham, 2006). For example, in the mega-diverse Brazilian Atlantic forest biome (Silva & Tabarelli, 2000), nearly half of all remaining forests are within 100 m from open habitats, and only < 30% is farther than 250 m from the nearest edge into core forest areas (Ribeiro *et al.*, 2009).

Here, we examine patterns of species replacement and nestedness in dung beetle assemblages across three spatial scales (i.e. among traps, within habitats and among habitats) in core areas and along edges of a large tract of primary forest, small forest fragments, sugarcane fields and cattle pastures in a human-modified Atlantic Forest landscape of north-eastern Brazil. We ask whether fragmentation-related effects and anthropogenic land use induce dung beetle assemblages to experience either homogenization, with species replacement within and among habitats decreasing in altered habitats (i.e. edge-affected and matrix habitats), or divergence. Homogenization would be supported by the occurrence of nested assemblages, whereas higher species replacement in edge-dominated and open habitats would be expected in the case of divergence.

To examine these predictions, we first investigate the extent to which dung beetle β-diversity varies in edge-affected habitats at different spatial scales. Second, we compare species replacement and nestedness using multiple measures of dissimilarity, accounting for compositional heterogeneity and pairwise comparisons deriving distance matrices controlling for the multivariate structure of dissimilarity (Baselga, 2010), both across traps (along the interior–exterior nonlinear gradient) and within and among habitats. Third, we document levels of taxonomic similarity between habitats based on ordination analyses. Finally, we discuss how species replacement and nestedness can be useful tools in improving sampling design in applied ecology studies.

METHODS

Study sites

The 66,700-hectare Serra Grande landscape is located within the Pernambuco Centre of Endemism, the most threatened ecoregion of the Brazilian Atlantic Forest (Silva & Tabarelli, 2000). Annual precipitation is ~2000 mm with a dry season

(< 60 mm per month) occurring from November to January and the wettest period between April and August (Pimentel & Tabarelli, 2004). This landscape contains approximately 9000 ha of forest (9.2% of total land cover) distributed across 109 forest remnants, ranging in size from 1.67 to 3500 ha, all of which are almost completely surrounded by fields of sugarcane monoculture (Silva & Tabarelli, 2000). The Coimbra Forest (3500 ha) is the largest Atlantic Forest remnant of north-east Brazil, which makes the Serra Grande landscape an excellent scenario to understand the long-term effects of habitat fragmentation on plant (Oliveira *et al.*, 2004; Santos *et al.*, 2008) and animal communities (Filgueiras *et al.*, 2011; Leal *et al.*, 2012). Coimbra is a large primary forest patch containing several large-seeded tree species and medium-sized frugivorous vertebrates, which have otherwise been almost completely extirpated from the entire region (Pimentel & Tabarelli, 2004). In addition to the dominant sugarcane fields, the study landscape contains other matrix types, such as cattle pastures and subsistence crops. However, Coimbra is not fully representative of a vast tract of continuous forest, which limits the comparative value of the best available baseline for our study design.

Survey effort was focused on 60 sampling units: 10 in core forest areas and 10 along the edges of the Coimbra forest remnant; 10 in sugarcane plantations and 10 in pastures, all of which were adjacent to the Coimbra forest; and 10 in small forest fragments and 10 in surrounding sugarcane plantation areas adjacent to small fragments (Fig. S1). We selected 50 small forest fragments with small (< 9000 m^2) or no core areas from which 10 fragments were drawn at random. As in previous studies (Santos *et al.*, 2008; Lopes *et al.*, 2009), we define core areas of forest interior as those beyond 200 m from the nearest forest edge. In this study, all sampling sites were spaced apart by at least 300 m (mean ± SD: 2910 ± 3320 m), which minimized any potential lack of spatial independence between sites.

Patch and landscape metrics

Fragment area was quantified using ArcView 3.2 (ESRI - Environmental Systems Research Institute, Redlands, CA, USA) and Erdas Imagine 8.4 (Leica Geosystems, Atlanta, Georgia, USA) on the basis of (1) three Landsat and Spot images (years 1989, 1998, 2003) and (2) a set of 160 aerial photographs (1 : 8000) taken from helicopter overflights commissioned in April 2003 (and funded by Conservação Internacional – Brasil). We measured the core area of each forest fragment to quantify the degree to which small patches used in this study were in fact edge-dominated. This was defined as the total remaining forest area once the 200-m buffer area had been subtracted.

Dung beetle sampling

Dung beetle surveys were carried out between October 2011 and February 2012. To avoid any potential climatic effect on dung beetle assemblages, trapping was carried out once at each site under comparable weather conditions, avoiding rainy days (Estrada *et al.*, 1999). In the interior of the Coimbra forest, each sampling unit consisted of four pairs of pitfall traps, set along a linear transect. Within forest areas, paired traps were set at distances of 15, 30, 60 and 120 m away from the nearest forest edge into core areas of the Coimbra forest or at the geometric centre of small fragments. Trapping within matrix habitats (cattle pastures and sugarcane plantations) were also set at 15, 30, 60 and 120 m from the nearest forest edge into the matrix (see Fig. S2). To reduce the effects of a lack of independence, paired traps along forest edges and matrix habitats were arranged according to an interior–exterior nonlinear gradient (see Fig. S2). Sampling arrays in all habitats were located randomly but always ensuring a minimum distance from one another of 300 m. Pitfall traps consisted of plastic containers (15 cm in diameter and 13 cm in height) with a bait-holding recipient (3 cm in diameter by 4.8 cm in height) containing ~30 g of human faeces. Dung beetle samples were collected 48 h after traps were installed and taken to the Serra Grande field station, where they were sorted into morphospecies. All dung beetles were then taken to the Insect Taxonomy and Ecology Laboratory at the Universidade Federal de Pernambuco (UFPE) for further identification and storage. Dung beetles were identified to species level at UFPE and Universidade Federal de Mato Grosso (UFMT), Brazil, and voucher specimens of all species are deposited at both entomological collections.

Data analysis

We assessed the compositional completeness of each habitat using EstimateS 9.1 (Colwell, 2013) by calculating the number of observed species as a percentage of the total richness, which was estimated based on the average of three abundance-based nonparametric estimators: Bootstrap, Chao 1 and Jack 1. To examine patterns of species replacement and nestedness at multiple scales, we used a species partitioning method [i.e. multiple-site dissimilarity metrics; Baselga (2010)] that allows the total Sørensen dissimilarity (beta diversity, $\beta_{SØR}$) to be separated into components of dissimilarity due to species replacements (i.e. turnover; β_{SIM}) and dissimilarity due to nestedness (β_{SNE}). We used the β_{SIM} (Simpson dissimilarity) (turnover component of Sørensen dissimilarity) and β_{SNE} (the nestedness component of Sørensen dissimilarity) (*sensu* Baselga, 2010):

$$\beta_{SIM} = \frac{b}{b+a} \text{ and } \beta_{SNE} = \left(\frac{c-b}{a+b+c}\right)\left(\frac{a}{2b+a}\right)$$

where a is the number of shared species between two cells, b is the number of species unique to the poorest site, and c is the number of species unique to the richest site.

We examined whether both species replacement and nestedness differed according to distances along the

interior–exterior nonlinear gradient, between edge-dominated habitats (small fragments and forest edges along the large primary forest patch), and the adjacent sugar cane plantation matrix using Kruskal–Wallis tests. To analyse the contribution of rare and abundant species on β-diversity (Chao *et al.*, 2012), we adopted the multiplicative diversity decomposition of the effective numbers of species (so-called Hill numbers, ^qD).

For S species, gamma (γ) diversity of order q is defined as:

$$^qD_\gamma = \left(\sum_{i=1}^{s} \bar{p}_i^{-q} \right)^{\frac{1}{(1-q)}}$$

where '*pi*' denotes the mean relative abundance of the *i*th species in *N* communities (Jost, 2007), and q is a parameter that determines the sensitivity of the measure to the relative abundances. The Hill number of order 1 was adopted, and each species was weighted according to its abundance (Jost, 2007).

Because this measure is undefined for $q = 1$, γ-diversity of order 1 can be estimated as:

$$^1D_\gamma = \exp \left(- \sum_{i=1}^{s} \bar{p}_i \log \bar{p}_i \right)$$

We also used pairwise dissimilarity (i.e. β_{sim} and β_{sne}) (*sensu* Baselga, 2010) between each pair of habitats and tested for a geographic distance effect using Mantel tests with 10,000 permutations.

To test whether dung beetle assemblages are taxonomically similar across the landscape, we used Non-metric Multidimensional Scaling (NMDS) ordinations of all 60 sites using their Bray–Curtis dissimilarity matrices with 1000 random restarts. Finally, we used analysis of similarities (ANOSIM – Clarke & Gorley, 2006) to test for significant differences in dung beetle assemblages in the landscape. NMDS ordinations and ANOSIM were carried out in PRIMER (Clarke & Gorley, 2006). Estimates of β-diversity and Mantel tests were carried out using the *betapart* (Baselga & Orme, 2012) and *ecodist* (Goslee & Urban, 2007) packages, respectively, in R version 3.1.0 (R Development Core Team, 2014).

RESULTS

Dung beetle species distribution

We recorded a total of 4218 dung beetles representing 45 species and 19 genera (Table S1). Comparisons with estimates of total species richness indicated that on average we detected 78% of all species present at each site (range = 73–84%) (Table S2). As expected, the number of species varied among habitats, being higher in forest sites (forest interior, forest edge and small fragments) than in matrix habitats (pastures around the Coimbra forest and sugarcane plantations around small fragments) (Fig. 1). The highest proportion of rare species – defined as those represented by singletons, (nine species, 45%) and restricted species that were present in only one habitat (seven species, 35%) – was found in forest edges and small fragments, respectively (see Fig. 1).

Patterns of species replacement and nestedness across scales

The percentage of shared species ranged from 20% between the Coimbra forest interior and small fragments, and between forest edges and small fragments, to 38% between forest interior sites and forest edges (Table 1). In terms of matrix habitats, dung beetle assemblages were highly uniform, with sugarcane plantations and pastures surrounding the Coimbra forest sharing the highest percentage of species (16%; Table 1).

As expected, species replacement was much higher within and among habitats than across traps (Table 2). At both the
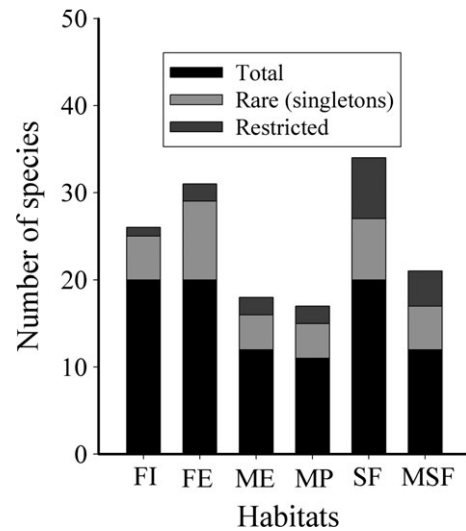

Figure 1 Total species richness and number of rare and restricted species in all habitat types sampled at the Serra Grande study landscape, Alagoas, Brazil.

Table 1 Matrix describing the percentages of species shared between habitat types sampled across the Serra Grande landscape, Alagoas, Brazil.

Locality (species richness)	FE (%)	MC (%)	MP (%)	SF (%)	MSF (%)
FI (20)	38	9	7	20	2
FE (20)		9	4	20	2
MC (12)			16	11	13
MP (11)				9	11
SF (20)					7

FI, Forest Interior; FE, Forest Edge; MC, Sugarcane matrix of the Coimbra Forest; MP, Pasture matrix of the Coimbra Forest; SF, small forest fragments; MSF, Sugarcane matrix of small fragments.

trap and habitat scales, forest interior showed the lowest species turnover. In general, edge-affected and adjacent matrix habitats increase the species replacement and decrease the nested pattern of dung beetle assemblages (Table 2). These patterns of β-diversity were also observed in the case of multiplicative diversity decompositions of Hill numbers (Table S3). In terms of the interior–exterior nonlinear gradient, there was a significant difference in nestedness (K–W-test $H = 4.74$, d.f. = 1, $P < 0.05$), but not in terms of species replacement (K–W-test $H = 2.1$, d.f. = 1, $P > 0.05$; Fig. 2 a–b). However, small fragments and adjacent sugarcane plantations did not exhibit any differences in either species replacement (K–W-test $H = 2.08$, d.f. = 1, $P > 0.05$) or nestedness (K–W-test $H = 3.5$, d.f. = 1, $P > 0.05$; Fig. 2 c–d). In addition, when we calculated pairwise β-diversity between sampling arrays using $β_{sim}$, forest and matrix habitats captured two clearly segregated species clusters (Fig. 3 a–b). On the other hand, patterns of β-diversity aggregation were unclear for forest edges and core forest interior, as well as for sugarcane plantations and pastures (Fig. 3 c–d).

Mantel tests failed to uncover any spatial effects on species replacement or nestedness (see Fig. S3). Both within and among habitats, dung beetle replacement and nestedness were not correlated with geographic distance (Fig. S3), indicating no large scale spatial structure on patterns of either replacement or nestedness (Table S4). In general, species replacement was most closely aligned with distance along forest edges and between forest edges and forest interior stands (Fig. S3). This was confirmed by a NMDS ordination

of sampling units based on both species composition and abundance, resulting in consistently segregated clusters of (a) forest edges, core areas of the Coimbra forest, and small fragments (Fig. 4a); (b) forest edges and core forest areas; and (c) a separate cluster formed by small fragments (Fig. 4b). This clear taxonomic segregation in dung beetle assemblages across the landscape, both in terms of abundance ($R = 0.67$, $P < 0.01$) and species composition ($R = 0.68$, $P < 0.01$), was further supported by ANOSIM tests.

DISCUSSION

Our results suggest that (1) each natural and anthropogenic habitat at the Serra Grande landscape supports a distinct set of dung beetle species; (2) there is a strong influence of fragmentation-related effects on dung beetle β-diversity, with species replacements increasing in altered habitats (i.e. increased β-diversity across edge-affected habitats); (3) although geographic distance among patches is a strong predictor of species replacements, edge effects enhance the taxonomic divergence of dung beetle assemblages; (4) dung beetle assemblages are clearly non-randomly distributed, with habitat type clearly associated with patterns of nestedness; and (5) dung beetle species replacement and nestedness are unrelated to geographic distance, implying that neighbouring sites are not necessarily more similar in their assemblage composition. Our findings also indicate that dung beetle assemblages tend to be reorganized in space according to the nature of anthropogenic habitats created by forest conversion.

Table 2 Relative contribution of species replacement ($β_{SIM}$) (*sensu* Baselga, 2010) and nestedness ($β_{SNE}$) (*sensu* Baselga, 2010) for the total dissimilarity values (i.e. Sørensen dissimilarity, 100%) of dung beetle assemblages across pitfall traps, habitat types and sampling arrays across the entire Serra Grande landscape, Alagoas, Brazil.

|	Sites	$β_{SIM}$ (%)	$β_{SNE}$ (%)
Traps	Forest interiors ($N = 80$)	65.4	34.6
	Forest edges ($N = 80$)	64.4	35.6
	Sugarcane matrix of primary forest ($N = 80$)	80.8	19.2
	Pasture matrix of primary forest ($N = 80$)	57.5	42.5
	Small fragments ($N = 80$)	94.2	5.8
	Sugarcane matrix of small fragments) ($N = 80$)	90.4	9.6
Within habitats	Forest interiors ($N = 10$)	73.3	26.7
	Forest edges ($N = 10$)	77.6	22.4
	Sugarcane matrix of primary forest ($N = 10$)	70.1	29.9
	Pasture matrix of primary forest ($N = 10$)	88	12
	Small fragments ($N = 10$)	87.3	12.7
	Sugarcane matrix of small fragments ($N = 10$)	91.7	8.3
Among habitats	Forest interiors + forest edges ($N = 20$)	85.4	14.6
	Forest edges + small fragments ($N = 20$)	93	7.0
	Forest edges + sugarcane ($N = 20$)	93.2	6.8
	Forest edges + pasture ($N = 20$)	93.1	6.9
	Forest edges + sugarcane + pasture ($N = 30$)	95.5	4.5
	Forest edge + forest interior + sugar cane + pasture ($N = 40$)	95.6	4.4
	Small fragments + sugarcane ($N = 20$)	94.4	5.6
	Matrix of primary forest, sugarcane + pastures ($N = 20$)	90.3	9.7
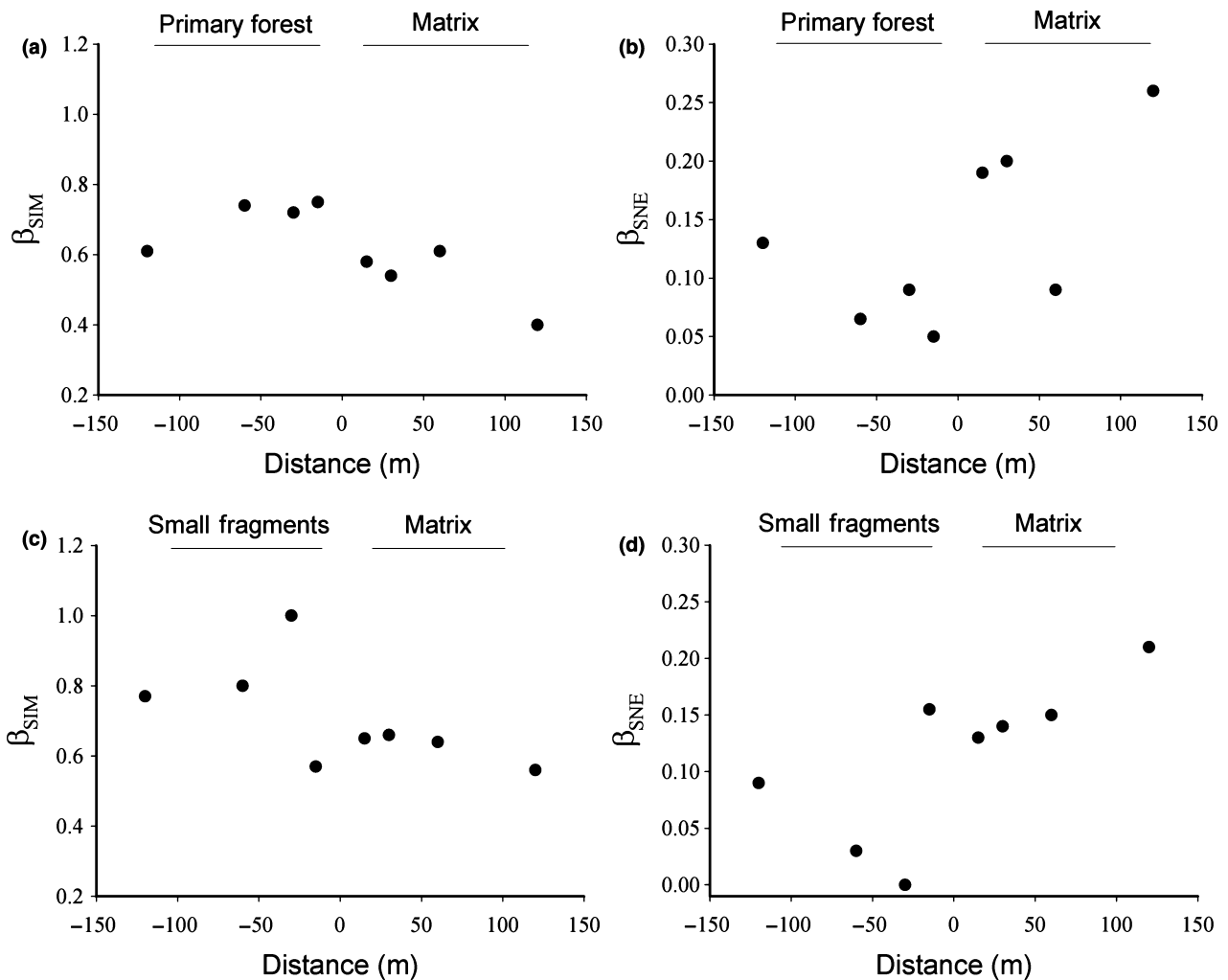
Figure 2 Species replacement (β_{SIM}) and nestedness (β_{SNE}) (i.e. multiple-site dissimilarity metrics) (*sensu* Baselga, 2010) of dung beetle assemblages according to varying distances along a nonlinear gradient sampled at the Serra Grande landscape; (a) and (b): forest edge of primary forest (negative distances) + pasture and sugarcane plantation matrices (positive distances); (c) and (d): small fragments (negative distances) and sugarcane plantation matrix (positive distances).

These findings, particularly the cross-habitat differences in taxonomic assemblages and greater levels of species replacements across edge-affected and matrix habitats, corroborate the hypothesis that plant and animal communities can experience taxonomic divergence in human-modified landscapes (Laurance *et al.*, 2007; Arroyo-Rodríguez *et al.*, 2013), particularly across edge-affected habitats. In fact, divergence is also expected to occur among communities inhabiting forest habitats in different landscapes, particularly those supporting contrasting habitat matrices in terms of vegetation structure and composition. In the Serra Grande landscape, however, we showed taxonomic divergence among dung beetle assemblages inhabiting forest habitats immersed within a single open-habitat matrix consisting of sugar cane fields and cattle pastures.

In the case of tropical tree assemblages, variation between patches related to edge effects and patterns of seed rain have been proposed as the underling forces behind community divergence or increased species replacement (Laurance *et al.*, 2007). Although we have not explicitly examined the under-

lying mechanisms, spatial turnover across habitat boundaries is potentially driven by a number of factors. As a general mechanism, we refer to (1) differences in dispersal ability exhibited by dung beetle species, particularly in traversing open habitats and (2) differences in patch accessibility due to the spatial configuration of habitats, the structural contrast between any given patch and the adjacent matrix, and the habitat quality of the matrix (see Ewers & Didham, 2006; Kindlmann & Burel, 2008; Uezu *et al.*, 2008; Uezu & Metzger, 2011). Specifically, more structurally isolated forest fragments and forest edges are likely to be accessed by only a small high-vagility subset of the dung beetle fauna (see Prevedello & Vieira, 2010; Filgueiras *et al.*, 2011), thereby supporting the notion of taxonomic distinctiveness and more divergent assemblages compared to sites immersed in the same continuous forest patch. On the other hand, well-connected patches tend to share a higher number of species as did forest edges and core areas of the Coimbra forest. This is consistent with the marked effect of habitat configuration
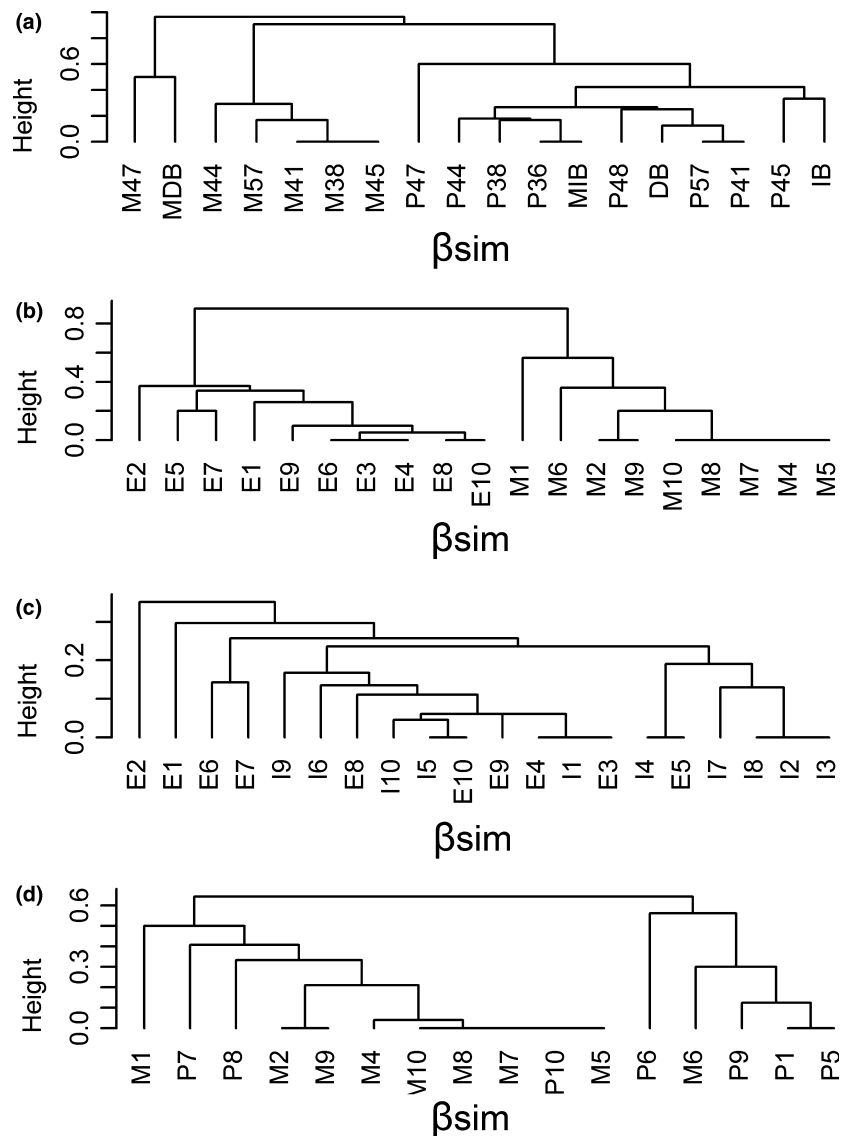
Figure 3 Clustering using average linkage of the β_{sim} components of species pairwise dissimilarity (*sensu* Baselga, 2010) between: (a) small fragments (P_{31}, P_{36}, P_{38}, P_{44}, P_{45}, P_{47}, P_{48}, P_{57}, P_{DB}, P_{IB}) + matrix (MP_{31}–MP_{IB}), (b) forest edges of primary forest (E_1–E_{10}) + matrix (M_1–M_{10}), (c) forest edges (E_1–E_{10}) + core forest interiors (I_1–I_{10}) of primary forest and (d) sugarcane plantation (M_1–M_{10}) + pasture matrix of primary forest (P_1–P_{10}) sampled at the Serra Grande study landscape.

within the overall landscape matrix on the species similarity of dung beetle assemblages in a Mediterranean system (Numa *et al.*, 2009).

In addition to between-habitat differences in accessibility and colonization probability, habitats also differ in terms of their intrinsic suitability for particular groups of dung beetle species in human-modified landscapes (Gardner *et al.*, 2008; Filgueiras *et al.*, 2015). Although differences in terms of habitat suitability may not result in either community-level divergence or homogenization, they can account for the distinct patterns of taxonomic assemblages within each habitat. At Serra Grande, forest fragments are surrounded by a uniform and inhospitable matrix of sugarcane monoculture, which is periodically burned (Santos *et al.*, 2008). Both small fragments and forest edges of large patches are more desiccated and wind-exposed and support a depauperate tree assemblage where light-demanding species become hyperdominant (Oliveira *et al.*, 2004). Adaptation to more illuminated and drier habitats likely explains the occurrence of few forest-

dependent beetle species (e.g. *Dichotomius* aff. *sericeus*, *Coprophanaeus dardanus*, *Oxysternon silenus*) but several disturbance-adapted species (e.g. *Canthon* aff. *piluliformis*, *Pseudocanthon* aff. *xanthurus*, *Trichilum externepunctatum*), which were restricted to sugarcane fields at Serra Grande. Structural differences between open and forest habitats can therefore largely explain patterns of community structure (Hanski & Cambefort, 1991). In human-modified Atlantic Forest landscapes, edge-affected habitats and open-habitat matrices are apparently only suitable for a very limited subset of generalist forest-dependent species in addition to disturbance-adapted species occurring almost exclusively in those habitats (see Filgueiras *et al.*, 2015).

Our results also support the notion that disturbed habitats differ in terms of species turnover. In particular, they indicate that dung beetle replacements were lower across small fragments and their adjacent matrix than along forest edges of a large remnant and its surrounding matrix. It has been proposed that multiple edges profoundly influence ecological
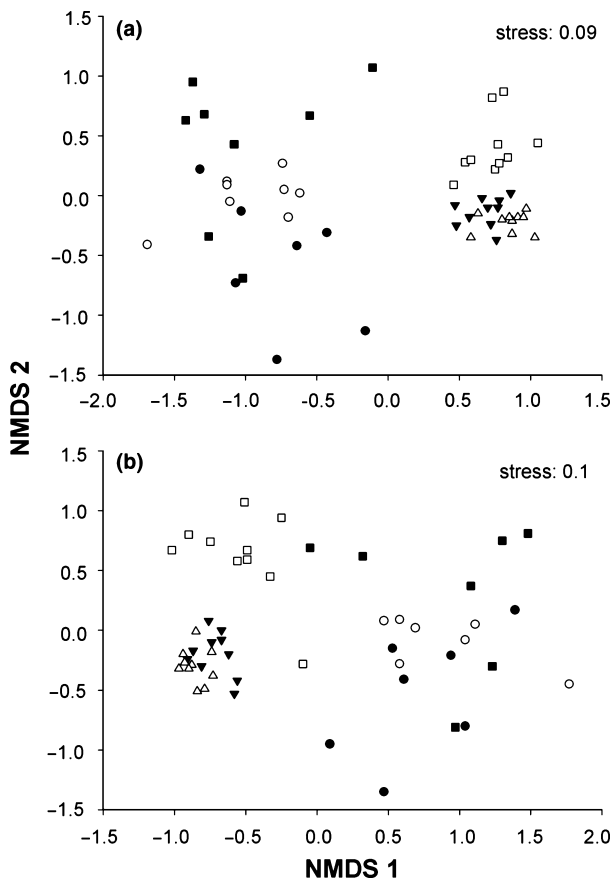
Figure 4 NMDS ordination based on the dung beetle community structure in terms of the abundance (a) and species composition (b) across different forest and matrix habitats. Forest edges (open squares) and sugarcane plantation (dark shaded squares) of small forest fragments, forest edge (dark shaded triangles), interior forest areas (open triangles), sugarcane plantation (open circles) and pastures (dark shaded circles) around the Coimbra forest.

patterns and processes within small forest patches (Malcolm, 1994; Fletcher *et al.*, 2007; Banks-Leite *et al.*, 2010), and theoretical models consistently predict that edge effects should occur on both the forest and matrix sides of the habitat boundary (Ewers & Didham, 2006). Therefore, environmental conditions in small fragments and the surrounding open-habitat matrix may converge due to pervasive edge effects, rendering both of these habitat types suitable to the same set of disturbance-adapted species. This form of abiotic homogenization can add to the drastic taxonomic homogenization among matrix habitats, resulting in a small matrix contribution to the overall gamma diversity of the entire landscape.

In synthesis, the consolidation of human-modified landscapes can radically reorganize the spatial structure of dung beetle assemblages as species replacements appear to be strongly influenced by habitat configuration, with higher β-diversity across edge-affected habitats. Although the conversion of once vast tracts of old-growth forests into human-modified landscapes, such as extensive monocultures

that provide low environmental heterogeneity, can result in biotic homogenization (Melo *et al.*, 2013), habitat fragmentation induced by anthropogenic land use can promote an alternative form of community-level taxonomic divergence. This likely results from a clearly non-random pattern of habitat selection of both forest-dependent and disturbed-adapted beetle species across the entire landscape, given decisive contrasts in species-specific habitat suitability. This community-level taxonomic divergence suggests that edge-dominated and matrix habitats ensure the persistence of disturbance-adapted species, some of which exclusively in these habitats, which are unsuitable for forest-dependent species. In other words, while the establishment of human-modified landscapes likely results in the local extirpation of forest-dependent species, it allows the persistence of disturbance-adapted species, which contributes to the overall diversity of the entire landscape. Accordingly, conservation planning should address all habitat components of landscapes (Rösch *et al.*, 2015), including remaining patches of old-growth forests, edge-affected habitats and regenerating forest patches (Solar *et al.*, 2015). This is particularly the case when disturbance-adapted species represent a substantial portion of the taxonomic, functional and/or phylogenetic diversity captured by the regional species pool. Further studies should investigate to what extent disturbance-adapted species contribute to arthropod diversity at local and regional scales as this question is central to the role played by human-modified landscapes as a long-term biodiversity repository.

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SUPPORTING INFORMATION

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

Figure S1 Map of the Usina Serra Grande landscape within the Atlantic Forest of northeastern Brazil showing the 60 sampling sites.

Figure S2 Schematic figure showing the sampling design used to quantify dung beetle assemblages along the interior-exterior non-linear gradient between forest edges and matrix habitats.

Figure S3 Results of Mantel tests showing the correlation between species turnover (β_{sim}) and nestedness (β_{sne}) of dung beetle assemblages with linear distances (m) for forest interiors (a, b), forest edges (c, d), small fragments (e, f), forest edges + forest interiors (g, h), and pastures + sugarcane plantation (i, j) of the Serra Grande landscape.

Table S1 Species and number of individuals of dung beetles sampled in the Atlantic forest study landscape, Alagoas, north-eastern Brazil.

Table S2 Observed species richness, abundance, and estimates of sampling completeness for dung beetles in the Atlantic forest study landscape, Alagoas, north-eastern Brazil.

Table S3 Dung beetle β-diversity (Mean $\pm$ SE) according to the multiplicative diversity decompositions of effective numbers of species (i.e. Hill numbers, $q = 1$) in the study landscape.

Table S4 Pairwise dung beetle β-diversity (β_{sim}) s and linear distances (km) to small forest fragments (a), forest edge and forest interior (b) and adjacent habitat matrices (c).

BIOSKETCH

Bruno K.C. Filgueiras conducted this work as part of his PhD at the Universidade Federal de Pernambuco. His research addresses determinants of community patterns and conservation biology of insects, with emphasis on tropical forests. Specifically, he is exploring the importance of anthropogenic land use and fragmentation-related effects on insect diversity at different scales.

Author contributions: B.K.C.F. and M. T. conceived the manuscript objectives. B.K.C.F. proceeded with data analysis and led the writing; M.T., I.R.L., C.A.P., F.Z.V.M. and L.I. contributed to the development of the idea and writing the manuscript.

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