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The relative influence of different landscape attributes on dung beetle communities in the Brazilian Atlantic forest



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ABSTRACT

Land-use change is considered the greatest threat to biodiversity worldwide. As such, identifying the drivers that shape biological communities is crucial for enhancing conservation strategies in human-modified tropical landscapes. We used a hybrid patch-landscape design and a multi model inference approach to assess the relative impacts of forest loss, increased edge density and increased pasture cover on dung beetle functional groups in the Brazilian Atlantic Forest – a biodiversity hotspot. Our findings provide novel empirical evidence showing that edge density can be a major driver for dung beetles when compared to forest and pasture cover at the landscape scale. However, forest and pasture cover also influenced some dung beetle responses, supporting the idea that biological communities are negatively affected by habitat loss and changes in land cover. We found that dung beetle body size, protibia area and metatibia length were all larger in landscapes with increased edge density, reinforcing the need for further studies exploring which mechanisms could favour the presence of larger dung beetles in fragmented tropical landscapes. Taken together, these results suggest the need of conservation and management strategies focused on the protection of the remaining Atlantic Forest fragments, and the promotion of forest recovery and reduction in the pasture cover and edge density at the landscape-level.

1. Introduction

Land-use change represents one of the major threats to global biodiversity (Newbold et al., 2019), altering species distributions and weakening ecosystem functionality (Cardinale et al., 2012; Pimm and Raven, 2000). Habitat loss – which reduces the available native core habitat and the functional/climate connectivity between patches (Senior et al., 2019), along with fragmentation impacts on remaining habitat structure (Laurance et al., 2006) and microclimate (Didham and Lawton, 1999) are suggested as the main pathways by which land-use change affects biodiversity in anthropogenic landscapes (Didham et al., 1998). This is particularly so in the tropics (Newbold et al., 2019), which host most of Earth's biodiversity and have the greatest rates of land-use change (Barlow et al., 2018; Lambin et al., 2003).

The historical trajectory of the Brazilian Atlantic Forest offers an

excellent opportunity to examine how land-use change is affecting tropical forest biodiversity (Melo et al., 2013). This forest hotspot is one of the most diverse ecosystems in the world (Myers et al., 2000), and has experienced high rates of habitat loss and fragmentation (Tabarelli et al., 2010). As a result of five centuries of deforestation, forests in this biome now covers only 11.7% of their original area, and 80% of forests are contained in fragments of 50 ha or less (Ribeiro et al., 2009; Ribeiro et al., 2011). Several studies have shown that Atlantic forest loss and fragmentation leads to profound ecological consequences such the loss of taxonomic and functional diversity (Audino et al., 2014), altered species composition (Filgueiras et al., 2011) and loss of carbon stocks (Rocha-Santos et al., 2016). These consequences are more alarming when they involve the loss of keystone groups, which can result in cascade effects with severe implications for ecosystem functioning (Morante-Filho et al., 2018). For example, the loss of vertebrate and

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Fig. 1. Study area in the Atlantic Forest biome, Brazil. (A) Localization of study area in which the communities of dung beetles were sampled in the state of Bahia, Brazil; (B) Distribution of the 16 landscapes (black circles) and characterization of the land-use in the study; (C) Example of the buffer of 1-km radius created around the fragment's center point for landscape descriptors calculations (i.e. forest cover, edge density and pasture cover).

invertebrate seed-dispersers can affect processes related to seed dispersal and seedling establishment (Culot et al., 2015), and consequently the ability of forest fragments to recover as well as to resist further disturbances.

Dung beetles are considered a responsive and cost-effective model system for evaluating the impacts of human activities on tropical ecosystems (Bogoni et al., 2019; Gardner et al., 2010; Nichols et al., 2007). They also contribute to important ecosystem processes such as soil nutrient cycling, secondary seed dispersal, and seedling establishment (França et al., 2018; Nichols et al., 2008). Hence, research shows that both their sensitivity to environmental changes and ability to contribute to ecosystem functioning are influenced by a set of functional traits such as the resource-relocation behaviour, body size, diet, and habitat preference (Barragán et al., 2011; Leite et al., 2018; Nichols et al., 2009). For instance, it has been demonstrated that forest loss affects dung beetle species according to their habitat preference (da Silva et al., 2019; Leite et al., 2018). It has also been found that smaller and isolated fragments have impoverished dung beetle communities (Filgueiras et al., 2011), but appear to serve as a refuge for some forest species (Arellano et al., 2008).

Despite advances provided by previous research investigating the impacts from habitat loss and fragmentation on biodiversity (Gardner et al., 2008), as well as assessing the dung beetle responses to land-use change (Filgueiras et al., 2015), there are two key knowledge gaps which limit the ability of promoting conservation strategies within

fragmented landscapes. First, few studies have evaluated how the contribution of different landscape descriptors may vary for different functional groups (Moura et al., 2015); and even fewer have considered morphological traits that may advance our understanding on how dung beetles respond to forest fragmentation (McGill et al., 2006). Second, when multiple landscape descriptors (e.g. patch size and shape) have been used to explain dung beetle responses, these descriptors were analysed individually (Campos and Hernández, 2015; Filgueiras et al., 2011) and/or at a patch scale (but see Filgueiras et al., 2015; 2016), and within other forest ecosystems (Arellano et al., 2008; Sánchez-de-Jesús et al., 2015).

Here, we addressed these knowledge gaps by surveying 16 landscapes and distinct dung beetle responses to assess how distinct landscape-level descriptors (e.g. forest cover, edge density, and pasture cover) affect tropical forest biodiversity. We ask the following questions: (1) How these landscape descriptors affect different dung beetle responses? and (2) What landscape descriptor was the main driver of ecological changes in dung beetle communities? We expect dung beetle responses to vary among the distinct landscape descriptors, given that dung beetle communities host large groups of species with different habitat and feeding needs, life history, and dispersal capabilities (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991). We also predict a compositional differentiation in dung beetle communities between landscapes, given their sensibility to habitat alteration (Barlow et al., 2010; Filgueiras et al., 2015) and the previous evidence that shows that changes in β -diversity can emerge in fragmented tropical landscapes (Filgueiras et al., 2016; Morante-Filho et al., 2015). We also expect forest cover to drive the most pervasive biological effects, as previous research highlights its importance when compared to other landscape descriptors (Fahrig, 2003; 2013; Pardini et al., 2010). Taken together, our analyses provide a quantitative understanding of the spatial attributes that may drive the persistence and loss of dung beetles in the Atlantic forest biodiversity hotspot and can provide a basis for predicting the biological consequences of future deforestation on other tropical forested regions.

2. Material and Methods

2.1. Study area

The study was conducted in the southern region of Bahia state, Brazil ($15^{\circ}280S$, $39^{\circ}150$ W, WGS84). This region is dominated by tropical lowland rainforest (Thomas et al., 1998), with mean annual temperature and rainfall of 24 °C and *ca*. 2.000 mm, respectively. Landuse changes were particularly severe within large tracts of previously continuous forests, which were converted to small fragments in different succession stages and embedded within a mosaic of different matrices such as cocoa plantations and cattle pastures (Pardini et al., 2009).

2.2. Sampling design and landscape descriptors

We selected 16 non-overlapping sampling landscapes (Fig. 1) based on a hybrid patch-landscape approach (Tischendorf and Fahrig, 2000). Landscape selection was based on high-resolution satellite images from 2009 to 2010 (RapidEye*), and 2011 (QuickBird* and WorldView*). The polygons were classified as forest fragments and different land-uses (e.g. pasture and other matrices), according to the Brazilian Institute of Geography and Statistics (IBGE, 2006). After ground-validation, we used ArcGIS 10.2 software (ESRI, 2011) to develop a digital map with a scale of 1:10 000 and covering an area of 3.500 km². The study area shows a subdivision into two regions (north and south, Fig. 1B), mainly due to a sandy stripe between them, because we avoided to sample in Restinga and Montane Forests. However, the two regions show similar vegetation types, soil and topography (Thomas et al., 1998).

We used the FRAGSTATS software (McGarigal et al., 2012) to estimate the percentage of forest and pasture cover in the matrix (hereafter 'pasture cover'), and the edge density in each landscape. Forest cover within our landscapes varied between 3 and 100%, pasture cover 0 and 100%, and edge density 0 and 73 m/ha (see Table S2 for details). The percentage of forest cover and edge density variables were based on forest fragments (old-growth and secondary forest) within a 1-km radius from the centre of the landscape - the same scale used for assessing the pasture cover. The centre of each landscape was selected preferably in a fragment of old-growth forest. We used a scale of 1-km radius to calculate forest cover, edge density and pasture cover because it represents the longest movement distance recorded for dung beetle species in Atlantic Forest within a 48-h period (da Silva and Hernández, 2015). Landscapes were separated by at least 1-km from the border of the buffer to assure independent dung beetle sampling (da Silva and Hernández, 2015).

2.3. Dung beetle data

Given that previous research within the Atlantic forest recorded greater dung beetle species richness and abundance during the rainiest months (Batista et al., 2016; Hernández and Vaz-de-Mello, 2009; Salomão and Iannuzzi, 2015), dung beetles were sampled three times at each of the 16 landscapes during the rainy season (April-June) in 2017. We used pitfall traps, which consisted of a plastic container (15 cm in diameter and 13 cm in height) buried with an opening at ground level and with a small bait container (3 cm in diameter by 4.8 cm in height). Pitfalls were filled with *ca*. 250 ml of a killing solution containing salt and a few drops of detergent; and were protected from rain by a plastic lid.

We established three sets of pitfalls, spaced 100-m apart (da Silva and Hernández, 2015), in the centre of each landscape. Each set contained three pitfalls disposed at the vertices of a 5-m equilateral triangle, and each trap had a different bait-treatment (*ca.* 30 g of either human faeces or decomposed meat, or non-baited) that was randomly allocated within sets. After 48 h, all sampled dung beetles were taken to *Laboratório de Ecologia Aplicada a Conservação* at the *Universidade Estadual de Santa Cruz, Brazil.* Thus, individuals were identified to species level, whenever possible and voucher specimens were deposited in the *Laboratório de Entomologia, Universidade Estadual de Santa Cruz, Brazil* and *Seção de Entomologia da Coleção Zoológica, Universidade Federal de Mato Grosso, Brazil.* We separated dung beetles according to their resource-relocation behaviour, diet preference, morphological traits and species composition.

2.3.1. Resource-relocation behaviour: Species were grouped as tunnelers, rollers and dwellers. This attribute is related to dung manipulation for feeding and reproduction (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991). Tunneler species are those that dig tunnels in the soil immediately under or very close to the resource, whereas rollers usually make resource balls and roll them to some distance from the original resources. Dwellers usually remain within the resource deposits.

2.3.2. Diet preference: Species were grouped as coprophagous, necrophagous and generalists. Following Beiroz et al. (2017), we considered as coprophagous and necrophagous when > 75% of the individuals of a given species was sampled in dung- or meat-baited traps, respectively; and as generalists those species with lower percentages. For species with less than five individuals, we sought the advice of the dung beetle specialist Dr Fernando Vaz-de-Mello.

2.3.3. Morphological traits: We examined morphological traits relevant to soil excavation and dung burial activities (Nichols et al., 2008; Petchey and Gaston, 2006). We used a Leica M250 microscope and Life Measurement software (*Leica, Wetzlar, Germany*) to measure the [i] body size (sum of pronotum and elytra length), [ii] protibia area, and [iii] metatibia length. We measured these traits in up to 30 individuals per species in each landscape (N = 1.450 individuals), which is the minimum threshold recommended for ensuring an accurate estimation of dung beetle mean trait values (Griffiths et al., 2016).

2.4. Statistical analyses

We used the coverage estimator recommended by Chao and Jost (2012) to estimate the accuracy of our dung beetle surveys. We considered not only the observed values of species richness, but also the expected values based on coverage-based extrapolations. We estimated the variance inflation factor (VIF) to assess collinearity among explanatory variables (presented in Table S3). Values of VIF should be < 2.5 in order to avoid the collinearity effect (Zuur et al., 2009).

To address our first question and assess the effects of the landscape descriptors (forest cover, edge density and pasture cover) on dung beetle responses (e.g. resource relocation behavior, diet preference and morphological traits), we adopted an information-theoretic approach based on the selection of the most parsimonious models (Burnham and Anderson, 2002). For each response metric, we built full models representing all combinations and interactions with explanatory variables. For each model, we computed the Akaike's information criterion corrected for small samples (AICc) and selected the most parsimonious models (Δ AICc < 4, when compared to the best model). From the complete set of possible models, we averaged coefficients of models within Δ AICc < 4, thus capturing greater uncertainty in the final set of candidate variables (Vierling et al., 2013). We fixed a Gaussian distribution for continuous response variables after verifying for

normality; and used Poisson distribution, corrected for over-dispersion (quasi-Poisson) if required, when response variables did not follow a normal distribution (Zuur et al., 2009). We assessed the distribution suitability and model fit through residual analysis and semivariograms (Crawley, 2012; Diggle and Ribeiro, 2007).

All response metrics were analyzed at landscape-level (i.e. three sets of pitfall traps per landscape). Models were run for species richness and abundance of each resource-relocation behaviour (tunnelers, rollers, and dwellers) and diet preference (coprophagous, necrophagous, and generalists). The species richness and abundance of each of these groups represented, respectively, the total number of species and individuals sampled across the three surveys conducted in each of the landscapes. For models assessing morphological traits (body size, protibial area, metatibia length), we considered the community average of the trait as our response variables. Therefore, changes in body size, protibia area and metatibia length represent the average variation of these traits for each landscape. Lastly, to examine changes in species composition, we performed a Jaccard similarity index to assess the compositional similarity of dung beetle communities between landscapes. We also performed similarity profile tests (SIMPROF) to evaluate whether dung beetle compositional similarity differed significantly between distinct landscapes ($\alpha = 0.05$).

To assess the independent contribution and relative importance of each landscape descriptor and evaluated if forest cover would contribute more than edge density and pasture cover for changes in dung beetle communities (second question), we performed a hierarchical partitioning (HP) analysis (Mac Nally, 2000; Murray and Conner, 2009) with all variables retained in the candidate set with best models from previous analysis. Competing models were evaluated based on R² goodness of fit, which allowed us to interpret the independent effects of each predictor as the proportion of explained variance. The effects' significance ($\alpha = 0.05$) was calculated using a randomization test with 1,000 interactions (Mac Nally, 2002).

We performed analyses in R software (R Core Team, 2019) and using the following packages for computing: (1) coverage estimator *entropart*; (2) variance inflation factor — *car*; (3) normality — *stats*; (4) model selection — *MuMIn*; (5) hierarchical partitioning — *hier.part*. Jaccard similarity index and SIMPROF were conducted in Primer software version 6.0 (Clarke and Gorley, 2006).

3. Results

We sampled 3,944 dung beetles from 16 genera and 37 species in the 16 landscapes (Table S1). Sample coverage was satisfactory in all landscapes (75–99% of the species recorded, Table S2), indicating that our sampling effort was adequate.

3.1. How landscape descriptors affect dung beetle responses?

Distinct dung beetle responses were affected by different sets of landscape descriptors (Table 1). Landscape metrics were not correlated (VIF < 2.5), which allowed us to independently evaluate their effects on dung beetle responses (Table S3).

3.1.1. Resource-relocation behavior

Model selection revealed strong support for the influence of edge density and pasture cover for all resource-relocation behaviours, and from forest cover on roller species (Fig. 2, Table S4, Fig. S1). We found that dweller abundance, and tunneler abundance and richness declined with increased pasture cover and edge density. The abundance of rollers declined with lower forest cover, and when the interaction of higher edge densities and more pasture.

3.1.2. Diet preference

Forest cover had a strong influence on all diet-based dung beetle groups (Fig. 2, Table S4, Fig. S1). The abundance of coprophagous

Table 1

AICc-based model selection for (i) resource-relocation behavior, (ii) diet preference and (iii) morphological traits. Multimodel inference based on a model with all explanatory candidate variables followed by model selection (FC – forest cover, ED – edge density, PC – pasture cover, ED + FC – interaction edge density and forest cover, ED + PC – interaction edge density and pasture cover). We show results of all models within Δ AICc < 4.

Dung beetle response	Model ranks	Model	AICc	ΔAICc	ω	Cumulative $\boldsymbol{\omega}$
Resource- relocation						
Tunneler abundance	1	РС	43.11	0.00	0.46	0.46
	2	ED	45.00	1.89	0.18	0.64
Roller abundance	1	ED + PC	44.68	0.00	0.49	0.49
	2	FC	46.30	1.62	0.22	0.71
Dweller abundance	1	ED	39.03	0.00	0.87	0.87
	2	PC	42.81	3.78	0.13	1.00
Tunneler richness	1	ED	34.21	0.00	0.72	0.72
	2	PC	36.06	1.85	0.28	1.00
Roller richness	1	Null	49.30	0.00	0.40	0.40
Dwellers richness	1	Null	49.14	0.00	0.29	0.29
Diet preference						
Coprophagous abundance	1	ED	37.31	0.00	0.68	0.68
	2	PC	40.78	3.46	0.12	0.80
Necrophagous abundance	1	FC	45.09	0.00	0.40	0.40
Generalist abundance	1	FC	42.64	0.00	0.61	0.61
Coprophagous richness	1	ED	40.37	0.00	0.64	0.64
	2	FC	43.60	3.23	0.13	0.77
Necrophagous richness	1	PC	45.64	0.00	0.46	0.46
Generalist richness Morphological traits	1	Null	48.85	0.00	0.33	0.33
Body size	1	ED	32.43	0.00	0.32	0.32
•	2	ED + PC	32.64	0.21	0.29	0.61
Protibia area	1	ED	38.14	0.00	0.42	0.42
	2	ED + FC	38.63	0.49	0.33	0.75
	3	ED + PC	41.76	3.63	0.07	0.82
Metatibia length	1	ED	38.14	0.00	0.32	0.32

beetles declined with increased edge density and pasture cover at landscape-level, while their richness declined with the increase of edge density and forest loss. We found necrophagous abundance and richness declining with forest cover loss and increasing with pasture cover, respectively. The abundance of generalist beetles was enhanced by increased forest cover.

3.2. Morphological traits

We found strong support for the influence of edge density on all examined traits. Dung beetle body size and protibia area were higher in landscapes with greater edge density, and when the interaction between edge density and pasture cover was present in the models (Fig. 2, Table S4, Fig. S1). Hence, protibia area was also positively related to the interaction of larger edges and pasture cover, and negatively affected when edge density interacted with forest cover. Lastly, landscapes presenting more edge density also had dung beetle species with higher metatibia lengths.

3.2.1. Species composition

According to Jaccard similarity index and SIMPROF analysis, species distribution clustered dung beetles into eight significantly distinct groups (Fig. 3). Three clusters were composed by species with a narrow distribution, which were recorded in only one or two landscapes and varied between 50 and 100% of similarity. One cluster was composed

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Abundance tunnelers









Richness tunnelers

ED

PC

FC





Richness coprophagous



Abundance necrophagous



Richness necrophagous



Abundance generalists





-1.5 -1.0 -0.5 0 0.5 1.0 1.5

ED

PC

FC

ED + FC

ED + PC

Protibia area



Metatibia lenght



Fig. 2. Model averaging of candidate models and confidence intervals within Δ AICc < 4 for resource relocation behavior, diet preference and morphological traits on effects of ED – edge density, PC – pasture cover, FC – forest cover, ED + FC – interaction edge density and forest cover, ED + PC – interaction edge density and pasture cover.

-1.5 -1.0 -0.5 0 0.5 1.0 1.5



Fig. 3. Dendrogram clustering dung beetles, according to Jaccard similarity index and map of occurrence to dung beetle species recorded in the 16 landscapes of Atlantic Forest, Brazil. Solid lines represent statistical differences between groups, based on SIMPROF analyses ($\alpha < 0.05$).

by species with wider distributions, and each species was recorded in \geq eight landscapes (57% of similarity). Two clusters were composed by species distributed mainly in landscapes with higher forest cover (\geq 45%) and low edge density (33 and 24 m/ha); displaying 33% and 14% of similarity, respectively.

3.3. What landscape descriptor was the main driver of ecological changes in dung beetle communities?

Overall, edge density was the most important landscape descriptor (accounting for 66% of the explanation and having eight significant contributions), followed by forest cover (33%; four significant effects), and pasture cover (16%; two significant effects; Fig. 4, Table S5). We also found edge density influencing all dung beetle responses when considering the independent contribution from each landscape descriptor in complete models that showed the highest percentage of explained deviance.

4. Discussion

This study contributes to our understanding of the drivers of change in biodiversity within fragmented tropical landscapes. Two findings deserve special attention. First, in a broader perspective, all measured landscape attributes played a key role in determining the dung beetle responses, supporting the idea that biological communities are influenced by different landscape attributes in the Brazilian Atlantic Forest. Moreover, landscapes with higher forest cover and lower edge density sustained dung beetle community with different requirements of diet



Fig. 4. Gray bars represents independent contribution of each explanatory variable (relative importance) on dung beetles in Atlantic Forest, Brazil. Black bars represent significant effects ($\alpha = 0.05$) as determined by the randomization test. Z-scores for the generated distribution of randomized and statistical significance is based on the upper 0.95 confident limit ($Z \ge 1.65$). Legend: PC – pasture cover, ED – edge density and FC – forest cover.

preference, body size and resource relocation behaviour. Second, changes in the dung beetle community were strongly influenced by edge density rather than by forest and pasture cover at the landscape scale. We discuss these results below.

4.1. How landscape descriptors affect dung beetle responses?

4.1.1. Resource-relocation behaviours

Our results demonstrated that all resource-relocation groups were negatively affected by increased edge density, and that pasture cover and forest loss bring negative effects for dung beetles – particularly roller species, reinforcing the negative ecological impacts from habitat loss and fragmentation on biodiversity (Barlow et al., 2010; Gardner et al., 2008).

The different dung beetle resource-relocation behaviours are considered as a strategy to facilitate species coexistence (Hanski and Cambefort, 1991) through reducing competition for food resources and coping with dung dissection - which are key factors influencing the survival of tropical dung beetles (Halffter and Edmonds, 1982). As forest loss and fragmentation has been associated with loss of native forest mammals (Canale et al., 2012), resource scarcity in highly fragmented landscapes is likely to create a competitive hierarchy for dung beetle resource-relocation behaviours. Overall, rollers and fast tunnelers are considered stronger competitors than slow tunneler and dweller species (Hanski and Cambefort, 1991). However, this strength hierarchy (rollers > tunnelers > dwellers) is combined with associated energetic costs, where stronger competitors such as roller species need more energy and, consequently, more resources (Halffter and Edmonds, 1982; Krell et al., 2003). The relocation and use of energy reserves to roll the food resource away in a short time span may, therefore, cause a reduction in individual fitness - mainly when food resources are scarce - through affecting beetles' physiological integrity (França et al., 2016a). Reductions in fitness of roller dung beetles – which usually dig shallower nests (Hanski and Cambefort, 1991), may be escalated by edge effects (e.g. increased soil temperature) particularly where forest fragments are within a matrix with very dissimilar vegetation structure (Bunyan et al., 2012; Harper, 2005; Ries et al., 2004).

4.1.2. Diet preference

We found the abundance and richness of necrophagous and coprophagous beetles decreasing in landscapes with higher values of forest loss, edge densities and pasture cover, while more generalist beetle individuals were sampled in landscapes with more forest cover. Dung beetles' diet preference can be influenced by different resource characteristics such as the physical and chemical characteristics, water and/ or fibre content, and the nutritional value of dung resources (Arellano et al., 2015; Gittings and Giller, 1998; Verdú and Galante, 2004). Irrespective of their diet preference and resource characteristics, our results are probably related to the fact that landscapes with higher forest cover sustain greater environmental and resource heterogeneity, thus supporting more dung beetle species (Navarrete and Halffter, 2008; Tscharntke et al., 2012). In addition, landscapes dominated by pasturelands are also more likely to have non-native herbivore dung (Steinfeld et al., 2006), which may favour generalist species while negatively affecting necrophagous dung beetles that frequently compete with others insect groups for carcasses (Jong and Chadwick, 1999) - a less frequent and more spatiotemporally limited resource (Halffter and Matthews, 1966).

4.1.3. Morphological traits

Many studies show that dung beetles decrease in body size within tropical disturbed forests (e.g. Filgueiras et al., 2011; França et al., 2016b; França et al., 2017) and are more prone to local extinctions (Gardner et al., 2008). However, we surprisingly found increased body size, protibia area and metatibia length within landscapes with higher values of edge density and pasture cover. There are two likely reasons that could explain the differences between our results and previous research. First, these findings could be associated with an increase in generalist species – which may be favoured by climatic (França et al., 2020a) and anthropogenic disturbances (Beiroz et al., 2017; Salomão et al., 2018). The mean body size of our generalist species in landscapes with high edge density was *ca.* 8.4 mm, while coprophagous species had body sizes of around 5.2 mm. On the other hand, in landscapes with low edge density, the mean size of a generalist and coprophagous beetles was *ca.* 7.8 and 7.9 mm, respectively. Thereby, because larger species

are expected to perform more ecological functions (Feer, 1999; Vulinec, 2002), further research would need to ascertain the mechanisms by which increased edge density could favour larger beetle species in the Atlantic forests, as well as whether generalist species could provide functional redundancy in relation to dung beetle functions. Second, methodological differences in trait measurement. Most studies demonstrating the loss of larger beetles measured their body mass (e.g. Audino et al., 2014; Filgueiras et al., 2011), while here we measured their length (see Methods) – which is a trait correlated with biomass (e.g. Radtke and Williamson, 2005).

4.1.4. Species composition

By demonstrating that habitat loss and fragmentation can affect the composition similarity of dung beetles, our study provides support that forest disturbances can act as an environmental filter to biological communities (Magura et al., 2018; Su et al., 2004). The loss of dung beetle species filtered out in the landscapes highly-affected by habitat loss and changes in land cover may result in cascading effects and further losses in their contribution to ecosystem functions. Previous research has demonstrated that changes in dung beetle species composition can affect important ecological processes (Slade et al., 2007) which may bring further implications for Atlantic forests regeneration through altering the spatial patterning and demography of plant species that depend on dung beetles as secondary seed dispersers (Lawson et al., 2012; Vulinec, 2002). Similar cascading effects were observed in our landscapes, as the decaying of fruit biomass triggered by landscapescale deforestation (Pessoa et al., 2016) negatively affected local diversity of forest birds (Morante-Filho et al., 2018), key vectors of seed dispersal (Cazetta et al., 2019; Menezes et al., 2016).

We call for further investigations on how these compositional changes and the loss of dung beetle functional groups in response to habitat loss could affect the resilience of Atlantic forest fragments to ongoing climatic and anthropogenic disturbances on this biome (Sundstrom et al., 2012). This is particularly important given recent evidence demonstrating that interactions between human activities and climate stressors can cause drastic losses in dung beetle communities and their contribution to dung removal and seed dispersal in tropical forests (França et al., 2020b).

4.2. What landscape descriptor was the best predictor of ecological changes in dung beetle communities?

Previous research has highlighted forest cover as the main driver of biological effects when compared to other landscape descriptors (Fahrig, 2003; 2013; Pardini et al., 2010), but recently there has been a growing debate about the relative role of habitat amount versus habitat configuration (Fahrig, 2017; Fahrig et al., 2019; Fletcher Jr. et al., 2018). Our study revealed that edge density had an additive effect with forest and pasture cover, which would refute suggestions by Fahrig (2017) that fragmentation research and edge effects are "zombie" ideas, while giving support to the influence of forest edges for the coleopterofauna (Magura et al., 2017). Furthermore, dung beetle attributes responded differently to distinct landscape metrics, suggesting many aspects of the landscape can influence ecological conditions.

There are good reasons to support the importance of edge effects for dung beetles.

Matrix composition has also been shown to be as important as forest loss when shaping dung beetle communities in Mexican forests (Sánchez-de-Jesús et al., 2015), and dung beetles are known for their high sensitivity to even small changes in forest structure (da Silva and Hernández, 2016) and low-level forest disturbances (Bicknell et al., 2014) that can occur through altered microclimatic conditions at the forest edge (Laurance et al., 2002; Ries et al., 2004). Moreover, habitat conditions (e.g. low relative humidity, high luminosity and greater temperature variability) can directly influence both the larvae and adult survival in dung beetles, which are dependent of ephemeral resources that become unusable when desiccated (Sowig, 1995); and have been shown to be negatively affected by anthropogenic edges in forested landscapes (Filgueiras et al., 2015; 2016; Spector and Ayzama, 2003).

We provide evidence that the importance of landscape descriptors can vary for distinct beetle responses. A previous study in the same landscapes have shown that while the local diversity of forest birds is positively influenced by forest cover, the increasing density of edges favoured generalist counterparts, thus depicting how different landscape metrics have pervasive but distinct influence on species assembly in anthropogenic landscapes (Morante-Filho et al., 2018). Thereby, we also support that further research should focus on different landscape descriptors and biological/functional metrics when assessing the impacts of habitat loss and fragmentation, or promoting conservation strategies within anthropogenic landscapes in the tropics (Solar et al., 2016).

5. Conclusion

Our research assessed the influence of three distinct landscape attributes for dung beetle communities from the Brazilian Atlantic forest hotspot (Myers et al., 2000). We found edge density as the main driver of biological changes, but both forest and pasture cover also significantly influenced many of the dung beetle responses. We, therefore, call for conservation and management strategies focused on the protection of the remaining Atlantic Forest fragments, and the promotion the forest recovery and reduction in the pasture cover and edge density at the landscape-level. This will be beneficial not only for dung beetles, which perform several key ecological processes (Franca et al., 2018; Nichols et al., 2007), but also for the other groups that usually respond similarly to human-induced forest disturbances in tropical regions such as birds and plants (e.g. Barlow et al., 2016; Ferreira et al., 2018; Morante-Filho et al., 2018). Nevertheless, given that tropical ecosystems are subject to multiple sources of stress such as climate change and local disturbances (Barlow et al., 2018; França et al., 2020a), conservation efforts will also require multiple but interdependent management actions at landscape level to attain long-term success.

CRediT authorship contribution statement

Thamyrys B. Souza: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization, Project administration, Funding acquisition. Filipe M. França: Methodology, Writing - original draft, Writing - review & editing. Jos Barlow: Methodology, Writing - original draft, Writing - review & editing, Supervision. Pavel Dodonov: Conceptualization, Methodology. Juliana S. Santos: Methodology, Visualization, Writing - review & editing. Deborah Faria: Conceptualization, Methodology, Writing - review & editing, Funding acquisition. Júlio E. Baumgarten: Conceptualization, Methodology, Writing - review & editing, Funding acquisition, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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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.2020.106534.

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