



Landscape composition shapes biomass, taxonomic and functional diversity of dung beetles within human-modified tropical rainforests

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Abstract

Habitat loss and land-use change in tropical forests have modified the composition and configuration of natural landscapes, driving biodiversity loss. Through studies covering different approaches to diversity and functional traits, a more holistic comprehension may be drawn regarding the effects of habitat transformation. In this study, we evaluated how the forest cover and landscape heterogeneity shape the taxonomic and functional diversity and biomass of dung beetles. Dung beetles were sampled in 16 landscape units of the “Los Tuxtlas” Biosphere Reserve (Mexico). We collected a total of 2396 individuals of 25 species in 14 genera. Taxonomic and functional diversity and biomass of dung beetles were positively related to the amount of primary forest and negatively related to increased landscape heterogeneity. These results indicate that tropical rainforests are highly sensitive to landscape transformation, which jeopardizes the different aspects of biodiversity. By showing the importance of evaluating different facets of biodiversity we conclude that implementing different landscape descriptors and different diversity components is a complementary and efficient approach to assessing the effects of landscape composition on dung beetles’ assemblages in tropical rainforests.

Implications for insect conservation Landscape composition plays a pivotal role in elucidating the various components that define the dung beetle community in tropical forests. Furthermore, it is of utmost significance to encompass a diverse array of biodiversity components, alongside species biomass, in order to comprehensively evaluate the impact of human-induced landscape transformation.

Keywords Anthropogenic landscapes · Bioindicators · Biodiversity · Community ecology · Forest fragmentation · Tropical landscapes

Introduction

The fragmentation and loss of tropical forests are one of the main threats to biodiversity (Barlow et al. 2016). Such transformations in the landscape are intrinsically related to decreases in the forest amount and changes in the landscape heterogeneity, whose modifications positively or negatively affect the abundance and distribution of organisms in space (Alvarado et al. 2017; Dunning et al. 1992; Ezcurra 2016). These processes generate changes, mainly in microclimate, resource availability, biotic interactions, among others (Bennet and Saunders 2010; Broadbent et al. 2008). Therefore, is necessary to understand the mechanisms associated with human-generated landscapes and their effect on different components of biodiversity.

When we talk about biodiversity, taxonomic diversity is one of the most studied components to explain the effect

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of landscape composition and configuration on community structure (Asaad et al. 2017; Magnusson et al. 2013). In general, studies show a decrease in the number of species in environments with greater disturbance (Laurance et al. 2014). Besides taxonomic diversity, which contemplates the number of species and their relative abundances, the functional diversity highlights as an approach focused on the distribution of the species according to their functions in the ecosystems (Cadotte et al. 2011; Díaz et al. 2007; Sekercioglu 2012). While taxonomic diversity represents the variation in community structure and complexity of biotic interactions; functional diversity assesses the type, range, and relative abundance of functional traits of the organisms present in a community that influence ecosystem functioning (Córdova-Tapia and Zambrano 2015; Weiher 2011). Among the functional traits of ecological communities, biomass is used as a proxy of flow energy and matter by assimilated resources through the food chain (Laurance et al. 1997; Nunes et al. 2016; Saint-Germain et al. 2007). Therefore, because biodiversity has many facets, using a single component can give an incomplete view of the mechanisms that shape the structure, dynamics and functioning of communities (Piccini et al. 2020; Rivera et al. 2021; Verdú et al. 2007a, 2007b).

Dung beetles are a highly diverse group in tropical environments (Hanski and Cambefort 1991; Scholtz et al. 2009). These insects provide important ecosystem services associated with nutrient cycling, secondary seed dispersal, and pollination (Andresen and Feer 2005; Nichols et al. 2008; Sakai and Inoue 1999). The ecosystem services provided by the dung beetles are related to the way they use the food resources (i.e. mammal feces), which allows them to be functionally classified into different trophic guilds (Chin and Gill 1996; Estrada 1998; Nichols et al. 2008). Furthermore, assemblage biomass is extremely important to assess the ecosystem services provided by the dung beetles in ecosystems, while the mass of species represents the amount of ecological function of dung beetles. This is because large-bodied species tend to provide more ecological functions (i.e. dung removal rates) (Nervo et al. 2014) when compared to small-bodied ones even with higher abundances (Barnes et al. 2014; Piccini et al. 2020).

Regarding the forest loss and fragmentation scenario, there is a trend toward a higher richness of dung beetles in landscapes with more amount of primary forest (Alvarado et al. 2017; Estrada et al. 1998; Sánchez de Jesús et al. 2016). In tropical rainforests, the decrease in the amount of native forests is commonly followed by the local extinction of large-bodied species, which are replaced by the small-bodied beetles (Gardner et al. 2008; Klein 1989; Nichols et al. 2007). Consequently, there is strong evidence indicating that anthropogenic disturbance in the tropics is associated to environmental filters that simplifies functional

diversity of the dung beetles (Barragán et al. 2011; Rivera et al. 2021; Souza et al. 2020). In addition to forest cover loss, it is important to consider the spatial heterogeneity due to land cover change also influences the taxonomic and functional diversity of dung beetles (Alvarado et al. 2017; Correa et al. 2021; Rivera et al. 2021). In environmentally unfavorable landscapes (e.g. the pasture lands that replace tropical rainforests), the increase of landscape heterogeneity results in a decrease of dung beetles' richness (Alvarado et al. 2017; Nichols et al. 2007). This is supposed to occur due to the limited amount of food resources available in open areas (i.e. mammal feces) (Garmendia et al. 2013). In addition, dung beetles have physiological limitations that unable them to tolerate the marked climatic differences between forested and non-forested environments (Giménez-Gómez et al. 2018, 2020). The deforestation of tropical rainforests may affect specific attributes of dung beetle assemblages (e.g. species richness, functional diversity, or biomass, see Filgueiras et al. 2021) or the whole traits of beetles' assemblages (Rivera et al. 2021; Souza et al. 2020). By analyzing the different aspects of beetle assemblages, we may present a broader comprehension of the tolerance levels of ecological communities facing landscape transformations.

Their high sensitivity to environmental variation and diversity of functions makes dung beetles an excellent model for studying how the functional diversity of organisms is affected by habitat loss and land-use change. The substitution of tropical and subtropical rainforests by livestock and agriculture represents an environmental barrier for forest-dweller dung beetles (Filgueiras et al. 2015; Giménez-Gómez et al. 2018; Salomão et al. 2020). Thus, assessing different components of biodiversity (i.e. taxonomic, biomass, and functional) in relation to landscape composition allows us to understand how species respond to environmental gradients and how their ecological role in landscapes might be affected (Derhé et al. 2016; Nunes et al. 2016; Pakeman 2014). In this study, we evaluate how the amount of forest and landscape heterogeneity (structured due to anthropogenic activities) influences the taxonomic diversity, functional diversity, and biomass of dung beetles in the northernmost portion of tropical rainforests in America. We expect that taxonomic diversity, functional diversity, and biomass (i.e. diversity components) to be positively related to an increase in the proportion of forest in the landscape, but negatively related to an increase in landscape heterogeneity. This is mainly because native species to tropical rainforest ecosystems are physiologically adapted to closed-canopy forests conditions (Giménez-Gómez et al. 2020) and that environments with more forest have greater resource availability (i.e. higher quantity and diversity of mammalian feces) (Estrada et al. 1998; Garmendia et al. 2013; Klein 1989). Moreover, because species body size is sensitive to habitat shifts (Filgueiras et al. 2011, 2021), we expect that

dung beetle biomass increase with increasing forest cover and decreases with increasing landscape heterogeneity caused by human activities in our study area.

Methods

Study area

The study area is located within “Los Tuxtlas” biosphere reserve (RBLT), south of Veracruz, in central-eastern Mexico. It is bounded by a mountain range located between latitudes 18° 05'N–18° 45'N and longitudes 94° 35'W–95° 30'W (Fig. 1). Los Tuxtlas represents the northern limit of tropical forest in Mexico (Rzedowski 1963). The climate is warm-humid, with an average annual temperature of 25°C and annual rainfall between 3000 and 4600 mm (Soto 2004), with two climatic seasons. A rainy period from June to February and a dry period from March to May (Guevara et al. 2000). The vegetation corresponds to the high evergreen forest, which is the predominant native vegetation in the region. However, due to social (e.g. marginalization) and anthropogenic (e.g. deforestation) factors, much of the forest cover in the area has been converted to crops and pasture in the last 50 years (Ávila-Bello et al. 2018; García-Aguirre et al. 2010; Von Thanden et al. 2018). Currently, there are *ca.* 2140 forest fragments in RBLT (i.e. comprising *ca.* 30% of the conservation unit land cover), which is highly fragmented in lowlands, with most of the larger patches distributed in

intermediate altitudes and highlands (Guevara et al. 2004; Vega-Vela et al. 2018).

2.2 Landscape selection and characterization

Through 200 modulated training points for the IDRISI® software system, we generated the land cover map in the study area using high-resolution multispectral images (QuickBird: 2.4 m resolution) from 2014. The map was transformed into raster format in ArcGIS® software to subsequently obtain the landscape composition (i.e. forest cover and landscape heterogeneity) (Ahuatzin et al. 2019).

We selected 16 buffers as landscape units (i.e. study unit), there were mosaics with the land cover classes: primary forest, secondary forest, riparian forest, pastures, fences, cultivated land, sand, roads, urban area, water bodies (Ahuatzin et al. 2019) (Fig. 1, Table S1). In each landscape unit, we determined a central point delimited by buffers of 1 km of diameter, as a minimum measure, biologically relevant to the dispersal of dung beetles (Salomão et al. 2018) due to the availability of the resource (i.e. mammals feces) (see Estrada and Coates-Estrada 2002; Garmendia et al. 2013; Woodcock et al. 2010). We calculated, for each study unit, primary forest cover (%) with a binary map (i.e. primary forest=1 or no primary forest=0) and landscape heterogeneity with Shannon's exponential index that quantifies heterogeneity based on the number and proportion of land covers in the buffer (i.e. effective land cover) (Corro et al. 2019).

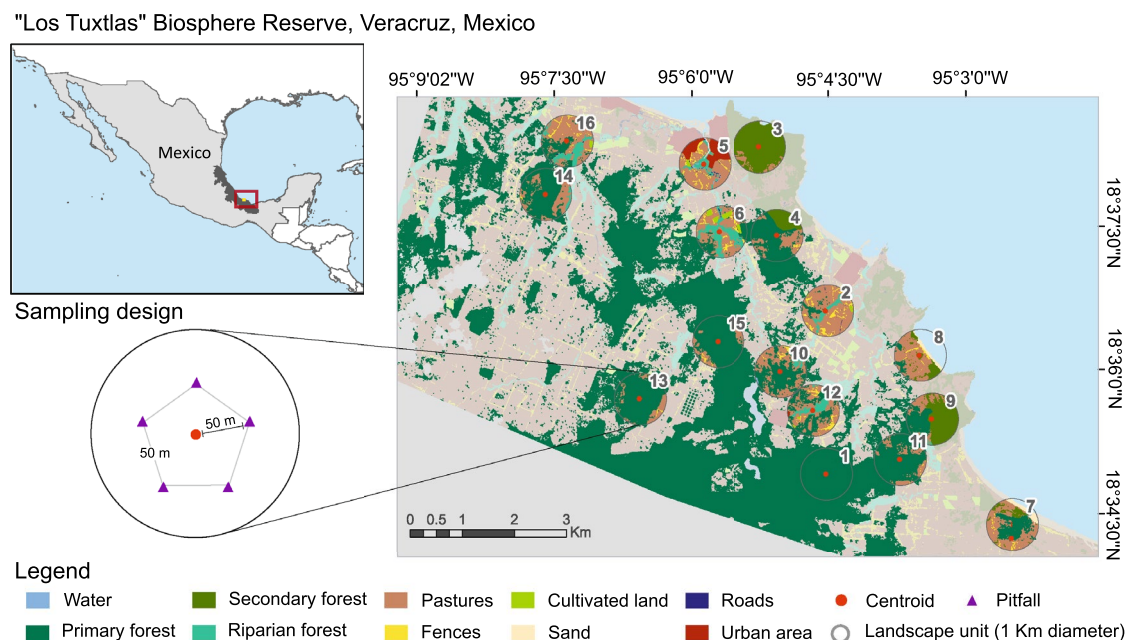


Fig. 1 Located off 16 sampled landscape units and land cover classification of the “Los Tuxtlas” Biosphere Reserve, state of Veracruz, Mexico (modified from Ahuatzin et al. 2019). The circles delimit the

1 km diameter landscape units, while red dots indicate the center of the landscape unit, and the purple triangles spaced 50 m where the dung beetles were collected

2.3 Beetles collection

We collected dung beetles between April to May 2016, sampling a pentagonal transects separated from each other by 50 m where each vertex we placed a pitfall, per study landscape unit on the land cover of forest (n= 60 pitfall in total, five per landscape unit) (Fig. 1). The pitfall consisted in a plastic container of 1 L (11 cm diameter and 14.3 cm high), to which we added 500 ml of solution (water, detergent, and salt). To attract the dung beetles, we used 50 g of human feces as bait (Salomão et al. 2018). The pitfalls were active for 48 h, subsequently the individuals were collected and preserved in 70% alcohol for determination. The collected material was deposited in the Entomological Collection of the Instituto de Ecología A.C. (IEXA) (Mexico).

a) Functional traits

We characterized the functional structure of the community using quantitative and qualitative traits that influences the ecosystem service provided by dung beetles (see Table S2 and S3, Barnes et al. 2014; Nichols et al. 2008). For quantitative traits we used linear morphological measurements (mm): head, pronotum, protibia, metatibia and elytra (Frantsevich 2010; Raine et al. 2018; Tong et al. 2005; Vaz-de-Mello et al. 2011) (Fig. S1). For qualitative traits we used activity period (i.e. diurnal and nocturnal) (Nichols et al. 2013) and resource relocation behavior to classify them into: paracoprids, telecoprids and endocoprids (Halffter and Edmonds 1982).

b) Biomass

We calculated total biomass per landscape unit as indicator of dung beetle community structure (Saint-Germain et al. 2007). We subjected two individuals per species to 45°C for 72 h in a drying oven and then weighed them on an analytical balance with a precision scale of 0.0001 g to obtain the mass. We obtained the total mean biomass per landscape unit using the formula:

$$Biomass = \sum_{i=25}^n m_i \cdot a_i$$

where m is mass measured in grams and a abundance for the species present in the landscape unit (Saint-Germain et al. 2007). We also obtained the mean body mass of each dung beetle species collected in the landscape units. With this approach, we aim to explain the loss of dung beetles in landscapes under a biomass scenario, which represent a proxy for the body size and removal rates of each specie (Nervo

et al. 2014). In this measure, we averaged the sum of the mass of dung beetles present in each landscape unit, without considering the abundance to represent the diversity of body mass in the landscapes. In this way, landscapes with higher mean body mass have larger beetles and tend to exhibits high dung removal than small beetles (Saint-Germain et al. 2007; Nervo et al. 2014). We obtained the mean body mass for each landscape unit using the formula:

$$Mean\ body\ mass = \frac{\sum_{i=1}^n m_i}{n}$$

where n is the total of species present in the landscape unit.

2.4 Data analysis

a) Taxonomic diversity

In each landscape unit we calculated the diversity based on Hill's numbers (Hseih et al. 2016). This metric is sensitive to taxonomic richness and relative abundance of species through the coefficient q , which was calculated for the diversity orders q^0 , q^1 , and q^2 . When Hill's number has a value of $q=0$ (q^0), represents the number of species collected (i.e. species richness), while if the value is $q=1$ (q^1) represents the Shannon–Wiener exponential index that express the number of typical species in the community (i.e. abundant species), and if is a value of $q=2$ (q^2) represents Simpson's inverse index that considers the abundance of the most abundant species within the community (i.e. dominant species, see Jost 2006; Moreno, 2000). We obtained the diversity values with the vegan package (R software version 2.5–3, Oksanen et al. 2018) (R Core Team 2021). The iNEXT package was used for evaluating the sampling coverage of the entire landscape (the total data, obtained from the 16 buffers) (R software version 2.0.19, Hseih et al. 2019). The sampling coverage was estimated according to the number of collected individuals.

b) Functional diversity

Functional diversity per landscape unit was evaluated through three indices: (i) functional richness ($FRic$) considers the distribution of species in the functional niche space, values close to zero indicate low diversity of functional traits in the community (Mason et al. 2005; Villéger et al. 2008; Carmona et al 2016); (ii) functional entropy ($RaoQ$) measures the distance between pairs of species considering the abundances of all species, high values indicate functional traits with varying while low values indicate dominance in abundance of similar traits (Botta-Dukát 2005); (iii) functional dispersion ($FDIs$) measures the distance of the

centroid (i.e. average of most abundant) with the traits, values varying between 0 and 1 where zero indicate low variety of functional traits versus most abundant traits (Petchey and Gaston 2002; Laliberte and Legendre 2010). We obtained functional diversity per landscape unit with package FD (R software version 1.0–12, Laliberté et al. 2014) (Laliberté and Legendre 2010).

c) Landscape composition and diversity analysis

We evaluated the effect of landscape composition on different biodiversity components of dung beetles with Generalized Linear Models (GLM). We used species richness (q^0), Shannon diversity (q^1), Simpson diversity (q^2), functional diversity (functional richness ($FRic$), functional entropy ($RaoQ$) and functional dispersion ($FDis$)), biomass and mean body mass as dependent variables. For independent variables we used primary forest cover and landscape heterogeneity (Table S4). Using the variance inflation factor (i.e. VIF), we found there was no collinearity between the independent variables (VIF = 1.83) with packages usdm (R software version 1.1–8, Naimi 2015). We verified a priori the normality of the data (i.e. Shapiro–Wilk test). Depending on the response (discrete or continuous), we fit the distributions of the models to different distribution types: Gaussian ($q^1, FRic, RaoQ, FDis$), Gamma (q^2 , biomass and mean body mass) and Poisson (q^0).

Results

We recorded 2 396 dung beetles belonging to 25 species and 14 genera (Table 1). The genera with more individuals was *Onthophagus* (31.5% of the total individuals) and *Canthon* was the genera with more species (20% of the total species). The four most abundant species (*Onthophagus batesi*, *Onthophagus rhinolophus*, *Canthon femoralis*, and *Canthon cyanellus*) together comprised ca. 50% of the total beetles collected in this study. Five species were rarely recorded (*Sulcophanaeus chryseicollis*, *Canthidium pseudopuncticolle*, *Canthon vazquezae*, *Eurysternus angustulus*, and *Pseudocanthon perplexus*), each one representing less than 1% of the total abundance. Regarding species distribution, *O. batesi* was recorded in all landscape units, followed by *C. cyanellus* ($n = 15$ landscapes). The species with narrowest spatial distribution were *Uroxys boneti* ($n = 3$ landscapes), *C. puncticolle* ($n = 2$), and *P. perplexus* ($n = 1$).

The species with more mass were *Coprophanaeus corythus* (0.347 g), *Deltochilum pseudoparile* (0.279 g), and

Dichotomius satanas (0.219 g), while *U. boneti* (0.002 g) had the lowest mass in our recorded data (Table S2). Nonetheless, when considering species abundance, *Phanaeus endymion*, and *C. corythus* were those with the highest species biomass (25% of the total biomass), while *C. pseudopuncticolle*, *U. boneti*, and *P. perplexus* were the species that had the lowest relative biomass (together comprising less than 0.5% of the total biomass) (Table S2). According to relocation of the resource, 14 species were paracoprid beetles, 8 species were telecoprid beetles, and 3 species were endocoprid. About the period of activity, 15 species were nocturnal, and 10 species were diurnal (see Table S2). The sample coverage indicated 100% completeness of dung beetles' assemblages at the sampling landscapes units (Fig. S2).

3.1 Landscape composition

Dung beetle diversity, biomass, mean body mass, and functional diversity varied positively respect forest cover. When the amount of forest was higher in the landscape, there was a higher species richness (q^0) ($\chi^2 = 13.98$, DE = 37.3%, $P < 0.001$), Shannon diversity (q^1) ($\chi^2 = 180.12$, DE = 72.7%, $P < 0.001$), Simpson diversity (q^2) ($\chi^2 = 5.30$, DE = 64.7%, $P < 0.001$), functional richness ($FRic$) ($\chi^2 = 0.91$, DE = 58.9%, $P < 0.001$), functional entropy ($RaoQ$) ($\chi^2 = 0.001$, DE = 69.9%, $P < 0.001$), functional dispersion ($FDis$) ($\chi^2 = 0.94$, DE = 56.5%, $P < 0.001$), biomass ($\chi^2 = 2.19$, DE = 19.8%, $P = 0.012$), and mean body mass ($\chi^2 = 8278.5$, DE = 49.2%, $P < 0.001$) of the dung beetles (Fig. 2). Nevertheless, when the heterogeneity was high in the landscape, there was a decrease in all response variables. Specifically, we observed that the increase of landscape heterogeneity presented a negative effect on species richness (q^0) ($\chi^2 = 20.09$, DE = 53.6%, $P < 0.001$), Shannon diversity (q^1) ($\chi^2 = 150.65$, DE = 60.8%, $P < 0.001$), Simpson diversity (q^2) ($\chi^2 = 4.49$, DE = 54.9%, $P < 0.001$), functional richness ($FRic$) ($\chi^2 = 0.003$, DE = 52.7%, $P < 0.001$), functional entropy ($RaoQ$) ($\chi^2 = 0.0007$, DE = 32%, $P = 0.0102$), functional dispersion ($FDis$) ($\chi^2 = 0.006$, DE = 27.2%, $P = 0.022$), biomass ($\chi^2 = 1.91$, DE = 17.3%, $P = 0.031$), and mean body mass ($\chi^2 = 4.6061$, DE = 35.6%, $P = 0.005$) (Fig. 3).

Discussion

We reported the relation between forest cover and landscape heterogeneity with the dung beetle assemblage of a highly fragmented high evergreen forest region in the “Los Tuxtlas” Biosphere Reserve (RBLT). In general, we show that different attributes of the dung beetle assemblage (i.e. taxonomic

Table 1 Distribution of the 25 species of dung beetle (Scarabaeidae) recorded in each of the 16 landscape units (LU) located within the “Los Tuxtlas” Biosphere Reserve, state of Veracruz, Mexico

Species	LU1	LU2	LU3	LU4	LU5	LU6	LU7	LU8	LU9	LU10	LU11	LU12	LU13	LU14	LU15	LU16	Total
<i>Ateuchus illaesum</i> (Harold, 1868)	7	0	10	2	0	0	0	0	0	0	0	1	0	0	6	0	26
<i>Bdelyopsis newtoni</i> (Howden, 1971)	0	0	2	5	0	0	0	0	0	0	0	113	13	0	0	0	133
<i>Canthidium centrale</i> (Boucomont, 1928)	3	21	36	17	0	0	14	0	7	0	41	4	23	1	5	0	172
<i>Canthidium pseudoperseptibile</i> (Kohlmann & Solis, 2006)	1	3	6	20	1	1	5	0	2	0	12	3	0	0	0	0	54
<i>Canthidium pseudopuncticolle</i> (Solis and Kohlmann, 2004)	0	0	0	0	0	11	0	0	0	5	0	0	0	0	0	0	16
<i>Canthon cyanellus cyanellus</i> (LeConte, 1859)	8	5	11	9	1	4	3	4	49	24	53	4	19	2	23	0	219
<i>Canthon eurysecelis</i> (Bates, 1887)	0	1	3	29	0	2	1	0	5	101	49	0	0	0	0	1	192
<i>Canthon femoralis</i> (Chevrolat, 1834)	6	148	7	0	0	0	45	0	0	4	1	0	2	3	1	3	220
<i>Canthon subhyalinus</i> (Harold, 1867)	0	0	1	5	0	1	0	0	6	7	7	0	1	1	2	1	32
<i>Canthon vazquezae</i> (Martinez, Halfitter & Halfitter, 1964)	5	0	1	0	0	0	0	0	0	0	0	0	1	0	7	0	14
<i>Copris laeviceps</i> (Harold, 1869)	8	5	44	18	0	4	0	0	17	0	45	4	5	1	11	5	167
<i>Coprophanaeus corythus</i> (Harold, 1863)	7	1	0	1	0	3	0	0	0	0	4	4	1	1	2	0	24
<i>Deltochilum sublaeve</i> (Bates, 1887)	5	0	0	0	0	0	0	0	0	0	10	0	1	13	1	0	36
<i>Deltochilum pseudoparile</i> (Paulian, 1938)	0	1	1	4	0	0	7	0	3	0	15	2	0	0	3	0	30
<i>Dichotomius satanas</i> (Harold, 1867)	10	0	0	0	0	0	0	0	0	0	1	1	2	13	1	0	28
<i>Eurysternus angustulus</i> (Harold, 1869)	3	0	0	0	0	0	0	0	0	0	1	1	3	2	3	0	13
<i>Eurysternus caribaeus</i> (Herbst, 1789)	1	7	5	6	0	0	9	0	4	2	2	1	5	4	3	0	49
<i>Eurysternus mexicanus</i> (Harold, 1869)	0	1	1	0	0	6	0	0	14	7	8	0	0	0	0	5	42
<i>Onthophagus batesi</i> (Howden & Cartwright, 1963)	5	16	1	26	31	198	10	5	9	25	23	24	44	48	5	8	478
<i>Onthophagus rhinolophus</i> (Harold, 1869)	9	0	53	30	0	6	0	0	7	5	43	20	33	6	7	59	278
<i>Phanaeus endymion</i> (Harold, 1863)	7	1	1	2	0	20	0	0	2	3	6	2	3	3	0	13	63
<i>Pseudocanthion perplexus</i> (LeConte, 1847)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Sulcophanaeus chryseicollis</i> (Harold, 1863)	11	0	1	1	0	1	0	0	0	0	2	1	1	1	1	0	20
<i>Uroxys boneti</i> (Pereira & Halfitter, 1961)	7	0	0	0	0	0	0	0	0	0	9	0	0	0	24	0	40
<i>Uroxys platypyga</i> (Howden & Young, 1981)	7	0	0	0	0	0	0	0	0	0	0	10	22	0	10	0	49
Number of individuals per LU	110	210	184	175	34	257	94	9	125	183	332	195	179	99	115	95	2396

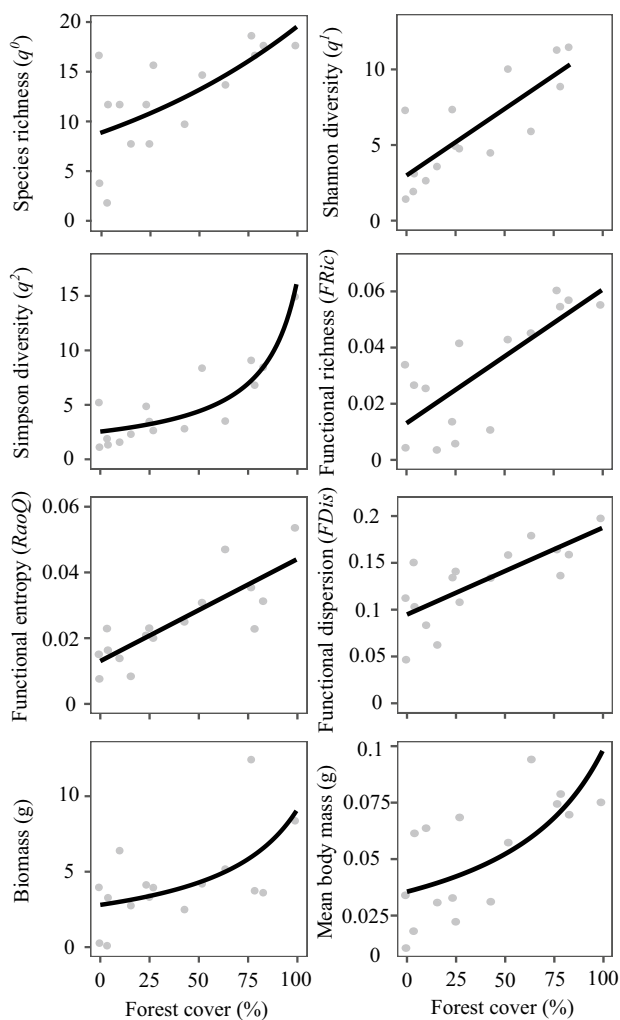


Fig. 2 Relationship between primary forest cover (%) and species richness (q^0), Shannon diversity (q^1), Simpson diversity (q^2), functional richness (*FRich*), functional entropy (*RaoQ*), functional dispersion (*FDis*), biomass and mean body mass. Each dot indicates a landscape unit of the “Los Tuxtlas” Biosphere Reserve ($n=16$), and the trend line represents the best fit distribution of the data. The value of functional richness is missing in LU8 because the data collected are not sufficient to assess it (see methods for more information)

diversity, functional diversity, and biomass) were positively related to the increase in the amount of forest and negatively associated with the rise in heterogeneity in the landscape. We demonstrated that the replacement of native tropical forests by other types of land cover had a homogeneous negative effect on different dimensions of diversity, besides decreasing the biomass of the dung beetles in the landscape. Our study reinforces previous findings in the region (Rivera et al. 2021; Salomão et al. 2020), suggesting the needing to conserve a large amount of forest in the tropical rainforests, as a fundamental habitat for the dung beetle assemblage.

Several studies have shown that the richness of dung beetles is lower in fragmented forests compared to continuous

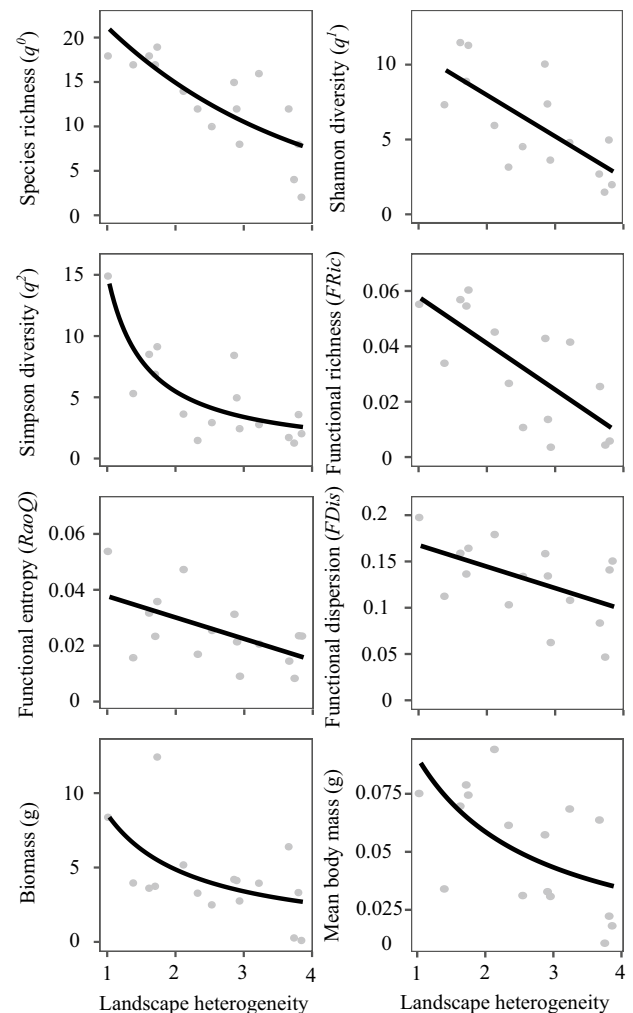


Fig. 3 Relationship between landscape heterogeneity and species richness (q^0), Shannon diversity (q^1), Simpson diversity (q^2), functional richness (*FRich*), functional entropy (*RaoQ*), functional dispersion (*FDis*), biomass and mean body mass. Each dot indicates a landscape unit of the “Los Tuxtlas” Biosphere Reserve ($n=16$), and the trend line represents the best fit distribution of the data. The value of functional richness is missing in LU8 because the data collected are not sufficient to assess it (see methods for more information)

forests, and decreases even more in open areas (i.e. pastures) (Derhé et al. 2016; Estrada et al. 1998; Estrada and Coates-Estrada 2002; Klein 1989). Their findings are consistent with the patterns observed in our landscape units, where we found a greater number of species as the amount of forest increases. Forested environments originally comprised the dominant native vegetation in the RBLT. Such vegetation physiognomy structure a closed-canopy ecosystem and maintain relatively low daily climatic fluctuations when compared to open environments (Antoniazzi et al. 2020; Davies-Colley et al. 2000). One important factor for the maintenance of dung beetle diversity is the availability of food resources. In this sense, the non-forested matrices

of the RBLT encompass different food resources that are often used by dung beetle species of tropical ecosystems (e.g. cattle dung in pasturelands, fruits in plantations, see Basto-Estrella et al. 2014; Halffter and Halffter 2009). Nonetheless, our results show an impoverished assemblage in landscapes with low amounts of forest cover, which only a few species may inhabit. Such species are open-habitat specialists (e.g. *P. perplexus*) or eurytopic species, which tolerates contrasting environmental conditions (e.g. *C. cyanellus* and *O. batesi*) (Bourg et al. 2016; Salomão et al. 2020). In tropical ecosystems, there is a marked environmental barrier settled by the decrease of forest cover, which is apparently driven by the physiological limitations of forest-dweller species. Studies in tropical ecosystems of America suggest that the thermoregulation strategies of dung beetle species (e.g. endothermic, ectothermic), together with their body traits (e.g. body size), are some of the main drivers of species spatial distribution (Giménez-Gómez et al. 2020; Verdú et al. 2007a, 2007b). Since the decrease in forest cover is followed by an increase in open vegetation, daily temperatures, and other restraining environmental attributes, the amount of forest cover is highlighted as an excellent proxy of anthropogenic disturbance in the tropics.

We also found that functional diversity (i.e. $FRic$, $RaoQ$, $FDis$) decreases when the amount of forest is low in the landscape. We report a loss of functional traits along a forest cover gradient, which could affect the ecosystem service provided by dung beetles provided (Derhé et al. 2016; Gagic et al. 2015). The increased functional dispersion ($FDis$) we report in the landscape with a greater amount of forest indicates the occurrence of specialist species of the forest. In tropical rainforests, the niche partitioning allows the maintenance of a high diversity of dung beetles, which are adapted to use different ranges of food resources (e.g. coprophagous, necrophagous, frugivorous, predators), periods of the day (e.g. diurnal, crepuscular, nocturnal), microclimates and periods of the year (Halffter and Halffter 2009; Hanski and Cambefort 1991; Larsen et al. 2006; Scholtz et al. 2009). Therefore, the assemblage of coprophagous beetles in landscapes with more forest indicates high diversity of functional traits to make use of the available resource; thus avoiding competition and allowing the coexistence between species (Barragán et al. 2011; Beiroz et al. 2018; Correa et al. 2019). As previously stated, it is important to consider that dung beetle assemblage in the RBLT may have reached a functional threshold (Rivera et al. 2021), and such limitation could be led by specific functional groups. Under such a scenario, the study of beetle diversity separated by functional groups has been revealing novel perspectives regarding community dynamics (see Bogoni et al. 2019; Souza et al. 2020). Therefore, to reveal sensitive species groups in fragmented landscapes from a functional perspective, future studies should focus on understanding how forest loss may

affect functional diversity by analyzing different functional groups.

The biomass and mean body mass of the dung beetles decrease when the amount of forest is lower in our landscape units. In other words, a decrease in abundance, and loss of large dung beetles (i.e. higher biomass) occurs in landscapes with less forest. Large-bodied species require a high amount of resources, and they are more sensitive to habitat change compared to small species (Barragán et al. 2011). In addition, the local extinction of large-sized mammals in the region of the RBLT (e.g. jaguar and tapir) apparently limit the availability of food resources and thus the distribution of larger dung beetles (Rivera et al. 2021). In this sense, here we present cues that landscape transformations can limit species distribution, and such filter excludes mostly the large-bodied dung beetles. Note that, there are anthropogenic ecosystems in which the hyper-abundance of small-bodied dung beetles can balance the decrease in biomass caused by the loss of larger species (Nichols et al. 2007), although this was not the case in our study. The loss of large-sized species implies decreasing the efficiency of the ecosystem services of dung beetles since there is no support that the small-bodied species compensate for the function provided by the large-sized dung beetles (Alvarado et al. 2018). In order to maintain functionally healthy forests, conservation policies should aim to increase dung beetle biomass and to maintain sensitive taxa that provide crucial ecosystem functions, as the large-bodied species.

Conversely, we found that landscape heterogeneity negatively affects the taxonomic and functional diversity, as well as the biomass, of dung beetles. As is well known, the landscape heterogeneity provides a mosaic with diverse environmental conditions that allow the permanence and coexists of species with different life histories and ecophysiological requirements (Turner et al. 2001). However, the heterogeneity of our landscapes is mainly caused by anthropogenic activities (e.g. pastures, crops, urban areas, etc.) (García-Aguirre et al. 2010). Therefore, it is expected that heterogeneous landscapes caused mainly by anthropogenic disturbances will negatively affect the diversity of groups of organisms (Laurance et al. 1997). Contrary to our findings, some studies report that the functional diversity of dung beetles can be high when environments are disturbed in some way (Beiroz et al. 2018) because they can make use of the resource in different land uses generated. We found a lower functional entropy value in landscapes with higher heterogeneity, due to a high abundance of similar functional traits (e.g. width of head and protibia). This result seems to indicate that heterogeneous landscapes in the RBLT are composed of functionally redundant species, which could exploit the spatial and trophic resources in a similar way, therefore increasing the competition among beetle assemblages. Furthermore, we found that the mean body mass of

dung beetles is lower as landscape heterogeneity increases, we suggest that small species could be favored in disturbed environments (Barragán et al. 2011; Salomão et al. 2018; Tilman et al. 1997; Woodcock et al. 2010), as large-bodied species are more susceptible to land-use changes.

In this study, we demonstrate the importance of integrating different biodiversity components in addition to species biomass to assess the effect of landscape transformation caused by human disturbance on dung beetle assemblages. Specifically, we observed that disturbed landscapes with low diversity of dung beetles also exhibited low diversity of their functions and lower biomass. These findings suggest that a complete view of biodiversity gives us a better picture of the effects of habitat loss, but also that the individualism of each its component indicates a different effect on ecosystem functioning. Overall, we show that the amount of forest cover positively affects dung beetle assemblages while landscape heterogeneity negatively affects them. We conclude that landscape composition is an important factor explaining different components that characterize the dung beetle community and that could shape the ecosystem services provided by dung beetles. These findings allow us to target tropical forest conservation strategies and mitigate the effects of heterogeneity caused by anthropogenic disturbances.

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Author contributions BR, WD, and JCLA conceived the research questions and designed the study. DA and EC collected the data. BR, DA, EC, and WD analyzed the data and led the writing of the manuscript. All authors have read and agreed to the published version of the manuscript.

Declarations

Competing interests The authors declare no competing interests.

References

- Ahuatzin DA, Corro EJ, Jaimes EJ, Armando-Aguirre J, Valenzuela-González JE, Feitosa RM, Ribeiro MC, Acosta LJC, Coates R, Dáttilo W (2019) Forest cover drives leaf litter ant diversity in primary rainforest remnants within human-modified tropical landscapes. *Biodivers Conserv* 28:1091–1107. <https://doi.org/10.1007/s10531-019-01712-z>
- Alvarado F, Escobar F, Williams DR, Arroyo-Rodríguez V, Escobar-Hernández F (2017) The role of livestock intensification and landscape structure in maintaining tropical biodiversity. *J Appl Ecol* 55:185–194. <https://doi.org/10.1111/1365-2664.12957>
- Alvarado F, Andrade ER, Santos BA, Prescott G, Souza G, Escobar F (2018) Forest cover is more important than farmland heterogeneity and livestock intensification for the retention of dung beetle phylogenetic diversity. *Ecol Ind* 93:524–532. <https://doi.org/10.1016/j.ecolind.2018.05.041>
- Andresen E, Feer F (2005) The role of dung beetles as secondary seed dispersers and their effect on plant regeneration in tropical rainforests. In: Forget PM, Lambert JE, Hulme PE, Vander Wall SB (eds) *Seed Fate: Predation, Dispersal and Seedling Establishment*. CABI International, Wallingford, pp 331–349
- Antoniazzi R, García-Franco J, Janda M, Leponce M, Dáttilo W (2020) Diurnal foraging ant–tree co-occurrence networks are similar between canopy and understorey in a Neotropical rain forest. *Biotropica* 52:717–729. <https://doi.org/10.1111/btp.12773>
- Asaad I, Lundquist CJ, Erdmann MV, Costello MJ (2017) Ecological criteria to identify areas for biodiversity conservation. *Biol Cons* 213:309–316. <https://doi.org/10.1016/j.biocon.2016.10.007>
- Ávila-Bello CH, Hernández-Romero AH, Mendoza-Briseño MA, Vázquez-Luna D (2018) Complex systems, agroecological matrices, and management of forest resources: an example of an application in Los Tuxtlas, Veracruz. *Mexico Sustain* 10:3496. <https://doi.org/10.3390/su10103496>
- Barlow J, Lennox GD, Ferreira J, Berenguer E, Lees AC, Nally RM, Thomson JR, Ferraz SF, Louzada J, Oliveira VHF, Parry L, de Castro R, Solar R, Vieira ICG, Aragão LEOC, Begotti RA, Braga RF, Cardoso TM, Raimundo CO, Souza CM Jr, Moura NG, Nunes SS, Siqueira JV, Pardini R, Silveira JM, Vaz-de-Mello FZ, Veiga RCS, Venturieri A, Gardner TA (2016) Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* 535:144–147. <https://doi.org/10.1038/nature18326>
- Barnes AD, Emberson RM, Krell F (2014) The role of species traits in mediating functional recovery during matrix restoration. *PLoS one* 9:e115385. <https://doi.org/10.1371/journal.pone.0115385>
- Barragán F, Moreno CE, Escobar F, Halfiter G, Navarrete D (2011) Negative impacts of human land use on dung beetle functional diversity. *PLoS one* 6:e17976. <https://doi.org/10.1371/journal.pone.0017976>
- Basto-Estrella GS, Rodríguez-Vivas RI, Delfín-González H, Reyes-Novelo E (2014) Dung beetle (Coleoptera: Scarabaeinae) diversity and seasonality in response to use of macrocyclic lactones at cattle ranches in the Mexican Neotropics. *Insect Conserv Diver* 7:73–81. <https://doi.org/10.1111/icad.12035>
- Beiroz W, Sayer E, Slade EM, Audino L, Braga RF, Louzada J, Barlow J (2018) Spatial and temporal shifts in functional and taxonomic diversity of dung beetles in a human-modified tropical forest landscape. *Ecol Ind* 95:518–526. <https://doi.org/10.1016/j.ecolind.2018.07.062>
- Bennett AF, Saunders DA (2010) *Habitat fragmentation and landscape change. Conservation biology for all*. Oxford University Press, Oxford, pp 88–106
- Bogoni JA, da Silva PG, Peres CA (2019) Roles of endothermy in niche differentiation for ball-rolling dung beetles (Coleoptera: Scarabaeidae) along an altitudinal gradient. *Ecography* 42:1803–1818. <https://doi.org/10.1111/j.1365-2311.2007.00907.x>
- Botta-Dukát Z (2005) Rao’s quadratic entropy as a measure of functional diversity based on multiple traits. *J Veg Sci* 16:533–540. <https://doi.org/10.1111/j.1654-1103.2005.tb02393.x>
- Bourg A, Escobar F, MacGregor-Fors I, Moreno CE (2016) Got dung? Resource selection by dung beetles in Neotropical forest fragments

- and cattle pastures. *Neotrop Entomol* 45:490–498. <https://doi.org/10.1007/s13744-016-0397-7>
- Broadbent EN, Asner GP, Keller M, Knapp DE, Oliveira PJC, Silva JN (2008) Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biol Cons* 141:1745–1757. <https://doi.org/10.1016/j.biocon.2008.04.024>
- Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *J Appl Ecol* 48:1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>
- Carmona CP, De Bello F, Mason NW, Lepš J (2016) Traits without borders: integrating functional diversity across scales. *Trends Ecol Evol* 31:382–394. <https://doi.org/10.1016/j.tree.2016.02.003>
- Chin K, Gill BD (1996) Dinosaurs, dung beetles, and conifers: participants in a cretaceous food web. *Palaios* 11:280–285. <https://doi.org/10.2307/3515235>
- Córdova-Tapia F, Zambrano L (2015) La diversidad funcional en la ecología de comunidades. *Ecosistemas* 24:78–87. <https://doi.org/10.7818/ECOS.2015.24-3.10>
- Correa C, Braga RF, Puker A, Korasaki V (2019) Patterns of taxonomic and functional diversity of dung beetles in a human-modified variegated landscape in Brazilian Cerrado. *J Insect Conserv* 23:89–99. <https://doi.org/10.1007/s10841-018-00118-6>
- Correa CMA, Ferreira KR, Puker A, Audino LD, Korasaki V (2021) Greenspace sites conserve taxonomic and functional diversity of dung beetles in an urbanized landscape in the Brazilian Cerrado. *Urban Ecosystems* 24:1023–1034. <https://doi.org/10.1007/s11252-021-01093-8>
- Corro EJ, Ahuatzin DA, Jaimes AA, Favila ME, Ribeiro MC, López-Acosta JC, Dáttilo W (2019) Forest cover and landscape heterogeneity shape ant–plant co-occurrence networks in human-dominated tropical rainforests. *Landscape Ecol* 34:93–104. <https://doi.org/10.1007/s10980-018-0747-4>
- Davies-Colley RJ, Payne GW, Van Elswijk M (2000) Microclimate gradients across a forest edge. *New Zealand J Ecol* 24:111–121
- Derhé MA, Murphy H, Monteith G, Menéndez R (2016) Measuring the success of reforestation for restoring biodiversity and ecosystem functioning. *J Appl Ecol* 53:1714–1724. <https://doi.org/10.1111/1365-2664.12728>
- Díaz S, Lavorel S, de Bello F, Quéfier F, Grigulis K, Robson TM (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proc Natl Acad Sci* 104:20684–20689. <https://doi.org/10.1073/pnas.0704716104>
- Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–175. <https://doi.org/10.2307/3544901>
- Estrada A, Coates-Estrada R (2002) Dung beetles in continuous forest, forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas, Mexico. *Biodivers Conserv* 11:1903–1918. <https://doi.org/10.1023/A:1020896928578>
- Estrada A, Coates-Estrada R, Dadda AA, Cammarano P (1998) Dung and carrion beetles in tropical rain forest fragments and agricultural habitats at Los Tuxtlas, Mexico. *J Trop Ecol* 14:577–593. <https://doi.org/10.1017/S0266467498000418>
- Ezcurra E (2016) Anthropogenic disturbances infiltrate forest fragments. *Proc Natl Acad Sci* 113:5150–5152. <https://doi.org/10.1073/pnas.1604829113>
- Filgueiras BK, Iannuzzi L, Leal IR (2011) Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest. *Biol Cons* 144:362–369. <https://doi.org/10.1016/j.biocon.2010.09.013>
- Filgueiras BK, Tabarelli M, Leal IR, Vaz-de-Mello FZ, Iannuzzi L (2015) Dung beetle persistence in human-modified landscapes: combining indicator species with anthropogenic land use and fragmentation-related effects. *Ecol Ind* 55:65–73. <https://doi.org/10.1016/j.ecolind.2015.02.032>
- Filgueiras BK, Peres CA, Iannuzzi L, Tabarelli M, Leal IR (2021) Recovery of dung beetle assemblages in regenerating Caatinga dry forests following slash-and-burn agriculture. *Forest Ecol Manage* 496:119423. <https://doi.org/10.1016/j.foreco.2021.119423>
- Frantsevich L (2010) Indirect closing of the elytra in a cockchafer, *Melolontha hippocastani* F. (Coleoptera: Scarabaeidae). *J Exp Biol* 213:1836–1843. <https://doi.org/10.1242/jeb.041350>
- Gagic V, Bartomeus I, Jonsson T, Taylor A, Winqvist C, Fischer C et al (2015) Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceed Royal Soci Biol Sci* 282:20142620. <https://doi.org/10.1098/rspb.2014.2620>
- García-Aguirre MC, Álvarez R, Dirzo R, Ortiz MA, Eng MM (2010) Delineation of biogeomorphic land units across a tropical natural and humanized terrain in Los Tuxtlas, Veracruz, Mexico. *Geomorphology* 121:245–256. <https://doi.org/10.1016/j.geomorph.2010.04.019>
- Gardner TA, Hernández MIM, Barlow J, Peres CA (2008) Understanding the biodiversity consequences of habitat change: the value of secondary and plantations forest of neotropical dung beetles. *J Appl Ecol* 45:883–893. <https://doi.org/10.1111/j.1365-2664.2008.01454.x>
- Garmendia A, Arroyo-Rodríguez V, Estrada A, Naranjo EJ, Stoner KE (2013) Landscape and patch attributes impacting medium- and large-sized terrestrial mammals in a fragmented rain forest. *J Trop Ecol* 29:331–344. <https://doi.org/10.1017/S0266467413000370>
- Giménez Gómez VC, Verdú JR, Gómez-Cifuentes A, Vaz-de-Mello FZ, Zurita GA (2018) Influence of land use on the trophic niche overlap of dung beetles in the semideciduous Atlantic forest of Argentina. *Insect Conserv Diversity* 11:554–564. <https://doi.org/10.1111/icad.12299>
- Giménez Gómez VC, Verdú JR, Zurita GA (2020) Thermal niche helps to explain the ability of dung beetles to exploit disturbed habitats. *Sci Rep* 10:1–14. <https://doi.org/10.1038/s41598-020-70284-8>
- Guevara SS, Laborde DJ, Sánchez-Ríos G (2000) La Reserva de la biosfera Los Tuxtlas (México). UNESCO, París
- Guevara S, Laborde J, Sánchez G (2004) Los Tuxtlas El paisaje de la sierra. Instituto de Ecología, Mexico
- Halfpter G, Edmonds WD (1982) The nesting behavior of dung beetles (Scarabaeinae): an ecological and evolutive approach. Instituto de Ecología AC, México
- Halfpter G, Halfpter V (2009) Why and where coprophagous beetles (Coleoptera: Scarabaeinae) eat seeds, fruits or vegetable detritus. *Boletín De La SEA* 45:1–22
- Hanski I, Cambefort Y (1991) Dung beetle ecology. Princeton University Press, Princeton
- Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol Evol* 7:1451–1456. <https://doi.org/10.1111/2041-210X.12613>
- Hsien T, Ma KH, Chao A (2019) Package ‘iNEXT’. iNEXT: iNterpolation and EXTrapolation for species diversity, R packages version 2.0.19
- Jost L (2006) Entropy and diversity. *Oikos* 113:363–375. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>
- Klein BC (1989) Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* 70:1715–1725. <https://doi.org/10.2307/1938106>
- Laliberté E, Legendre P, Shipley B, Laliberté ME (2014) Package ‘FD’. Measuring functional diversity from multiple traits, and other tools for functional ecology, R package version 1.0–12
- Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305. <https://doi.org/10.1890/08-2244.1>

- Larsen TH, Lopera A, Forsyth A (2006) Extreme trophic and habitat specialization by Peruvian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Coleopt Bull* 60:315–324. [https://doi.org/10.1649/0010-065X\(2006\)60\[315:ETAHSB\]2.0.CO;2](https://doi.org/10.1649/0010-065X(2006)60[315:ETAHSB]2.0.CO;2)
- Laurance WF, Laurance SG, Ferreira LV, Rankin-de Merona JM, Gascon C, Lovejoy TE (1997) Biomass collapse in Amazonian forest fragments. *Science* 278:1117–1118. <https://doi.org/10.1126/science.278.5340.1117>
- Laurance WF, Sayer J, Cassman KG (2014) Agricultural expansion and its impacts on tropical nature. *Trends Ecol Evol* 29:107–116. <https://doi.org/10.1016/j.tree.2013.12.001>
- Magnusson WE, Braga-Neto R, Pezzini F, Baccaro F, Bergallo H, Penha J et al (2013) Biodiversity and integrated environmental monitoring. Attema Design, California
- Mason NW, Moullot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111:112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>
- Moreno CE (2000) Métodos para medir la biodiversidad. Volumen 1. Manuales y tesis SEA
- Naimi B (2015) Packages USDM: Uncertainty analysis for species distribution models. R Package Version 1:1–15
- Nervo B, Tocco C, Caprio E, Palestini C, Rolando A (2014) The effects of body mass on dung removal efficiency in dung beetles. *PloS one* 9:e107699. <https://doi.org/10.1371/journal.pone.0107699>
- Nichols E, Larsen T, Spector S, Davis AL, Escobar F, Favila M et al (2007) Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. *Biol Cons* 137:1–19. <https://doi.org/10.1016/j.biocon.2007.01.023>
- Nichols E, Spector S, Louzada J, Larsen T, Amezcua S, Favila ME, Network TSR (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biol Cons* 141:1461–1474. <https://doi.org/10.1016/j.biocon.2008.04.011>
- Nichols E, Uriarte M, Bunker DE, Favila ME, Slade EM, Vulinec K et al (2013) Trait-dependent response of dung beetle populations to tropical forest conversion at local and regional scales. *Ecology* 94:180–189. <https://doi.org/10.1890/12-0251.1>
- Nunes CA, Braga RF, Figueira JEC, Neves FDS, Fernandes GW (2016) Dung beetles along a tropical altitudinal gradient: environmental filtering on taxonomic and functional diversity. *PLoS One* 11:e0157442. <https://doi.org/10.1371/journal.pone.0157442>
- Oksanen J, Guillaume-Blanchet F, Friendly M, Kindt R, Legendre P, McGinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2018) Package Vegan. Community Ecology Package. R package version 2.5–3
- Pakeman RJ (2014) Functional trait metrics are sensitive to the completeness of the species' trait data? *Methods Ecol Evol* 5:9–15. <https://doi.org/10.1111/2041-210X.12136>
- Petchey OL, Gaston KJ (2002) Functional diversity (FD), species richness and community composition. *Ecol Lett* 5:402–411. <https://doi.org/10.1046/j.1461-0248.2002.00339.x>
- Piccini I, Caprio E, Palestini C, Rolando A (2020) Ecosystem functioning in relation to species identity, density, and biomass in two tunneller dung beetles. *Ecological Entomology* 45:311–320. <https://doi.org/10.1111/een.12802>
- R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>
- Raine EH, Gray CL, Mann DJ, Slade EM (2018) Tropical dung beetle morphological traits predict functional traits and show intraspecific differences across land uses. *Ecol Evol* 8:8686–8696. <https://doi.org/10.1002/ece3.4218>
- Rivera JD, da Silva PG, Favila ME (2021) Landscape effects on taxonomic and functional diversity of dung beetle assemblages in a highly fragmented tropical forest. *Forest Ecol Manage* 496:119390. <https://doi.org/10.1016/j.foreco.2021.119390>
- Rzedowski J (1963) El extremo boreal del bosque tropical siempre verde en Norteamérica continental. *Vegetatio* 11:173–198. <https://doi.org/10.1007/BF00298831>
- Saint-Germain MICHEL, Buddle CM, Larrivee M, Mercado A, Motchula T, Reichert E et al (2007) Should biomass be considered more frequently as a currency in terrestrial arthropod community analyses? *J Appl Ecol* 44:330–339. <https://doi.org/10.1111/j.1365-2664.2006.01269.x>
- Sakai S, Inoue T (1999) A new pollination system: Dung-beetle pollination discovered in *Orchidantha inouei* (Lowiaceae, Zingiberales) in Sarawak, Malaysia. *Am J Bot* 86:56–61. <https://doi.org/10.2307/2656954>
- Salomão RP, Gonzalez-Tokman D, Dattilo W, López-Acosta JC, Favila ME (2018) Landscape structure and composition define the body condition of dung beetles (Coleoptera: Scarabaeinae) in a fragmented tropical rainforest. *Ecol Ind* 88:144–151. <https://doi.org/10.1016/j.ecolind.2018.01.033>
- Salomao RP, Favila ME, Gonzalez-Tokman D (2020) Spatial and temporal changes in the dung beetle diversity of a protected, but fragmented, landscape of the northernmost Neotropical rainforest. *Ecol Indic* 111:105968. <https://doi.org/10.1016/j.ecolind.2019.105968>
- Sánchez-de-Jesús HA, Arroyo-Rodríguez V, Andresen E, Escobar F (2016) Forest loss and matrix composition are the major drivers shaping dung beetle assemblages in a fragmented rainforest. *Landscape Ecol* 31:843–854. <https://doi.org/10.1007/s10980-015-0293-2>
- Scholtz CH, Davis ALV, Kryger U (2009) Evolutionary biology and conservation of dung beetles. Pensoft Publishers, Sofia, Bulgaria
- Sekercioglu CH (2012) Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. *J Ornithol* 153:153–161. <https://doi.org/10.1007/s10336-012-0869-4>
- Soto M (2004) El Clima. In: Guevara SS, Laborde DJ, Sánchez-Ríos G (eds) Los Tuxtlas: El paisaje de la sierra. Instituto de Ecología AC, México
- Souza TB, França FM, Barlow J, Dodonov P, Santos JS, Faria D, Baumgarten JE (2020) The relative influence of different landscape attributes on dung beetle communities in the Brazilian Atlantic forest. *Ecological Indicators* 117:106534. <https://doi.org/10.1016/j.ecolind.2020.106534>
- Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–1302. <https://doi.org/10.1126/science.277.5330.1300>
- Tong J, Sun J, Chen D, Zhang S (2005) Geometrical features and wettability of dung beetles and potential biomimetic engineering applications in tillage implements. *Soil Tillage Res* 80:1–12. <https://doi.org/10.1016/j.still.2003.12.012>
- Turner MG, Gardner RH, O'Neill RV, O'Neill RV (2001) Landscape ecology in theory and practice. Springer, New York, pp 1–23
- Vaz-de-mello FZ, Edmonds WD, Ocampo FC, Shoolmeesters P (2011) A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the new world (Coleoptera: Scarabaeidae). *Zootaxa* 2854:1–73. <https://doi.org/10.11646/ZOOTAXA.2854.1.1>
- Vega-Vela V, Munoz-Robles CA, Rodriguez-Luna E, Carlos Lopez-Acosta J, Serna-Lagunes R (2018) Analysis of landscape fragmentation in the Los Tuxtlas Biosphere Reserve, Veracruz, Mexico. *Ecosistemas Recursos Agropecuarios* 5:227–238
- Verdú JR, Arellano L, Numa C, Micó E (2007a) Roles of endothermy in niche differentiation for ball-rolling dung beetles (Coleoptera:

- Scarabaeidae) along an altitudinal gradient. *Ecol Entomol* 32:544–551. <https://doi.org/10.1111/j.1365-2311.2007.00907.x>
- Verdú JR, Moreno CE, Sánchez-Rojas G, Numa C, Galante E, Halfiter G (2007b) Grazing promotes dung beetle diversity in the xeric landscape of a Mexican biosphere reserve. *Biol Cons* 140:308–317. <https://doi.org/10.1016/j.biocon.2007.08.015>
- Villéger S, Mason NW, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301. <https://doi.org/10.1890/07-1206.1>
- Von Thaden JJ, Laborde J, Guevara S, Venegas-Barrera CS (2018) Forest cover change in the Los Tuxtlas biosphere reserve and its future: the contribution of the 1998 protected natural area decree. *Land Use Policy* 72:443–450. <https://doi.org/10.1016/j.landusepol.2017.12.040>
- Weiher E (2011) A primer of trait and functional diversity. In: Magurran AE, McGill BJ (eds) *Biological diversity frontiers in measurement and assessment*. Oxford University Press, Oxford, pp 175–193
- Woodcock BA, Redhead J, Vanbergen AJ, Hulmes L, Hulmes S, Peyton J et al (2010) Impact of habitat type and landscape structure on biomass, species richness and functional diversity of ground beetles. *Agr Ecosyst Environ* 139:181–186. <https://doi.org/10.1016/j.agee.2010.07.018>

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