

Ecology

Temporal changes of taxonomic and functional diversity in dung beetles inhabiting forest fragments and pastures in Los Tuxtlas Biosphere Reserve, Mexico

Cambios temporales de la diversidad taxonómica y funcional en los escarabajos del estiércol que habitan fragmentos de bosque y pastizales en la Reserva de la Biosfera Los Tuxtlas, México

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Abstract

We evaluated short- (among months within-years) and long-term (between 1999-2000 and 2016-2017) temporal patterns of taxonomic and functional β -diversity (and its components of substitution and gain/loss) of dung beetle assemblages in forest fragments and pastures in the Los Tuxtlas Biosphere Reserve (LTBR). Habitat type affected the taxonomic dissimilarity and the richness difference component, with average values being respectively 1.42 and 1.56 times higher in pastures than in forest fragments. Only habitat type was important for functional richness, being 1.93 and 1.69 higher in forest fragments than pastures in 1999-2000 and 2016-2017, respectively. Pastures were taxonomically and functionally poorer but were also more temporally dynamic than forest fragments both within-year and between-years. Habitat type is a determining factor for temporal dynamics, with forest fragments presenting more stable dung beetle assemblages than cattle pastures.

Keywords: Anthropogenic landscape; Bioindicators; Habitat modification; Scarabaeinae; Temporal patterns

Resumen

Evaluamos los efectos temporales a corto (entre meses de cada año) y largo (1999-2000 y 2016-2017) plazo sobre la diversidad β taxonómica y funcional (y sus componentes de sustitución y pérdida/ganancia) de los ensambles de escarabajos del estiércol en fragmentos forestales y potreros en la Reserva de la Biosfera Los Tuxtlas (RBLT). El tipo de hábitat afectó la disimilitud taxonómica y el componente de diferencia de riqueza de especies (diversidad β), con valores promedios de 1.42 y 1.56 veces más altos en los potreros que en los fragmentos forestales, respectivamente. Solamente el tipo de hábitat fue determinante para la riqueza funcional, siendo 1.93 y 1.69 veces más alto en los fragmentos forestales que en los potreros en el 1999-2000 y en el 2016-2017, respectivamente. Los potreros fueron taxonómica y funcionalmente más pobres, aunque también fueron temporalmente más dinámicos que en los fragmentos forestales, tanto dentro de cada periodo anual, como entre años. El tipo de hábitat es un factor determinante para las dinámicas temporales y se nota que las selvas son ambientes más estables que los potreros para los ensambles de los escarabajos del estiércol.

Palabras clave: Paisajes antrópicos; Bioindicadores; Cambios de hábitat; Scarabaeinae; Patrones temporales

Introduction

Biodiversity is constantly changing throughout time (Dornelas et al., 2014). Depending on the temporal scale analysed, different processes drive the maintenance of the ecological communities (Castillo-Escrivà et al., 2020). When analysing changes in species diversity throughout a year (i.e., short-term scale), it is expected that the interaction between seasonal variation and the surrounding environment determines how species diversity changes (Tonkin et al., 2017). For example, in a study performed with dung beetles in the Amazon region it was observed that the environment type modulated the seasonal variation of these insects' diversity (Noriega et al., 2021). On the other hand, when analysing biodiversity changes at long-term scale (e.g., changes in diversity between different decades), environmental characteristics related to ecological stability seems to be the strongest driving force in this temporal scale (Lindholm et al., 2020). In environments with unstable conditions for native biota, as pasturelands created in tropical rainforest biomes, there is a tendency towards more heterogeneous communities at long-term scales when compared to more stable ecosystems, as the native vegetation of a region (Salomão et al., 2020). Nonetheless, trends regarding different temporal scales are still incipient. By understanding how diversity changes behave at short- and long-term scales, we may comprehend and compare temporal contexts and depict if certain changes are related to seasonal variations (i.e., short-term scale) or to landscape stability contexts (i.e., long-term scale).

Anthropogenic activities are causing global biodiversity declines over time (Barlow et al., 2016; Newbold et al., 2015, 2020) and the replacement of native forests by agricultural land, such as pastures, is one of the main

causes of the global biodiversity crisis (Laurance et al., 2014). This process reduces species richness and tends to homogenize the species composition in anthropogenic land uses, with severe consequences to taxonomic (Newbold et al., 2015; Solar et al., 2015), functional (Flynn et al., 2009; Rivera et al., 2021), and phylogenetic diversity (Edwards et al., 2015; Rivera et al., 2022). Especially in the tropics, agricultural practices have led to marked landscape transformations, with the replacement of more than half of native forest cover of many tropical forest ecosystems (Myers et al., 2000; Ribeiro et al., 2009; Vega-Vela et al., 2018). This phenomenon has risen major concerns because tropical forests are key ecosystems that harbour at least two-thirds of the global terrestrial biodiversity and provide important economic goods and ecosystem functions (Gardner et al., 2009). Therefore, anthropogenic land-use changes are now considered one of the most important environmental threats for biodiversity in the Anthropocene (Dirzo et al., 2014).

There are several different approaches to understand how community heterogeneity (i.e., β -diversity) is established across short- and long-term temporal scales (Legendre, 2019; Magurran et al., 2019; Tatsumi et al., 2021). By partitioning β -diversity into its 2 mainly studied components (i.e., richness difference/nestedness and replacement) it is possible to understand how community heterogeneity is being structured (Legendre, 2014). Previous studies suggest that an equilibrium between replacement and nestedness components is more related to well-preserved areas (Solar et al., 2015), while an increase in species substitution (i.e., turnover or replacement) is associated to more unstable environmental conditions (Salomão et al., 2020). There are scarce studies comprising the effects of habitat type and different time-scale studies on ecological communities from a β -diversity perspective.

This is particularly alarming if we consider more than one facet of diversity (e.g., taxonomic and functional). Considering the ongoing scenario of native forest loss in tropical ecosystems (Hansen et al., 2020; Laurance, 2007), it is urgent to present different approaches that allow us to understand how biodiversity changes throughout years in the Anthropocene. Through the assessment of β -diversity approach, it is possible to understand how different environments may maintain biodiversity and stability of the ecological communities throughout years.

In both forest and pasture areas, dung beetles (Coleoptera: Scarabaeinae) are key components because they use dung for feeding and nesting. Due to this activity the dung beetles have meaningful roles in important ecosystem functions, such as nutrient recycling, bioturbation, secondary seed dispersal, plant growth enhancement, parasite control, and reduction of greenhouse gas emissions (Nichols et al., 2008; Slade et al., 2016). The loss of these functions and services is expected to have important effects on the ecosystem functioning (Braga et al., 2013; Slade et al., 2007). Besides, dung beetles are a diverse group of insects (taxonomically and functionally) that have been widely used to evaluate the effects of anthropogenic changes caused to natural environments, especially in tropical forests where they are cost-effective, responsive study models and biodiversity bioindicators (Barlow et al., 2010; Solar et al., 2015). These beetles also show a markedly seasonal pattern in response to climate conditions (temperature and precipitation) and availability of food resources (Hernández & Vaz-de Mello, 2009; Neves et al., 2010). Besides, few studies have evaluated dung beetle response to disturbance and habitat change over large time scales. Such studies present clear shifts in community structure throughout time (Escobar et al., 2008; Noriega et al., 2021), as well as an increase in dung beetle diversity with the increase of vegetation cover (Cuesta & Lobo, 2019). Therefore, both short- and long-term evaluations of dung beetle assemblages throughout time are helpful to understand how functional groups have changed among habitats and the underlying implications to conservation and management caused by habitat changes in ecosystem functioning.

Here, we evaluated the same dung beetle assemblages, sampled monthly in forest fragments and pastures in 1999-2000 and 2016-2017, aiming to unveil short- and long-term changes in functional diversity and taxonomic and functional composition in the Los Tuxtlas Biosphere Reserve (LTBR). We hypothesize that long-term effects on dung beetle assemblages (“between year β -diversity”) will be different than those assemblages analysed under short-term time scales (“within year β -diversity”). Moreover, we predict greater changes in pastures than

forest fragments due to higher temporal microclimatic stability (da Silva et al., 2019; Vega-Vela et al., 2018). Specifically, we expect: *i*) higher temporal taxonomic and functional changes in pastures than forest fragments driven by species/traits substitution (the same number of species/traits being gained and lost) rather than species/traits gain/loss (species/traits only being gained or only being lost in a nested way); and *ii*) higher taxonomic than functional β -diversity between sampling years (between year β -diversity) than among months of each sampling year (within year β -diversity).

Material and methods

The study was carried out in the Los Tuxtlas Biosphere Reserve (LTBR), located in the state of Veracruz, Mexico, within the municipalities of Catemaco, Hueyapan de Ocampo, San Andrés Tuxtla, and Santiago Tuxtla (18°20'-18°43' N, 95°07'-95°25' W; see Favila [2005] and Salomão et al. [2020] for maps of the study area and geographic coordinates of sites). The LTBR harbours some of the last rainforest remnants of the northernmost Neotropical region (UNESCO, 2020). Similar to other tropical regions, Los Tuxtlas has suffered high rates of deforestation (Guevara et al., 2000). Created in 1998, the LTBR ranges from coastal to higher elevations of the Sierra de Los Tuxtlas (from zero to 1,720 m asl) and spans across an area of 155,122 ha, which comprises 3 volcanoes: San Martín Pajapan, San Martín Tuxtla, and Santa Marta (Guevara et al., 2004). The mean annual temperature is 25 °C and precipitation ranges from 1,200 to 4,200 mm, directly related to elevation (Gutiérrez-García & Ricker, 2011). The landscape of LTBR was originally covered by tropical rainforest in lowlands and montane cloud forest in highlands (Favila, 2004; Guevara et al., 2000). The current landscape matrix in the LTBR comprises mainly agricultural land (pastures and fruticulture) (Guevara et al., 2000; Vega-Vela et al., 2018).

The forest fragments and pastures sampled in this study are located between the San Martín Tuxtla Volcano and the Sierra de Santa Marta Volcano (i.e., 2 nuclei areas). The elevation of the sites sampled ranges between 150-870 m asl (average \pm SD = 554.7 \pm 239.9 m), comprising both forest fragments and pastures. Temperature and precipitation were similar in both sampling years during the sampled months (Supplementary material: Fig. S1). For more details see Favila (2005) and Salomão et al. (2020).

We sampled the same 11 forest fragments and 6 pastures in 1999-2000 and 2016-2017. The data used in this study were obtained by Favila (2005) (data from

1999-2000) and Salomão et al. (2020) (data from 2016-2017). Both habitats were sampled monthly at each period almost at the same time, allowing us to compare the dung beetle assemblages between sampling periods and among months. We used baited pitfall traps to collect dung beetles in forest fragments and pastures. Pitfall traps (11 cm diameter \times 7.5 cm depth) were baited with *ca.* 25 g of human faeces and carrion (i.e., fish meat) separately. Each trap was filled with *ca.* 200 mL of 70% alcohol to catch and preserve the sampled specimens and covered with a plastic plate to prevent rainfall and leaf litter from falling into the trap. We installed 2 sets of 4 traps per site, with traps spaced out 20 m from each other within each group, alternately baited with faeces and carrion. Each set of traps was spaced out 100 m apart. Traps were placed at a distance of at least 20 m from the edge of the habitat surveyed (i.e., forest fragment or pasture), which is sufficient to observe clear differences in the dung beetle assemblage of forest fragments and pastures within the LTBR (Favila, 2005). Traps were left in the field for 48 h in every sampling period. At each period (i.e., 1999-2000 and 2016-2017), a total of 816 traps was set (8 traps per site \times 17 sites \times 6 months): 528 in forest fragments and 288 in pastures. Specimens were identified by comparison with the entomological collection of the Instituto de Ecología, A.C. in Xalapa, Mexico, where they were also deposited. A detailed description of the sampling design can be found in Salomão et al. (2020).

Dung beetle species were characterized in terms of 4 biological attributes used to calculate the functional diversity metrics: food relocation behaviour (rollers, tunnellers or dwellers), diet (coprophagous, necrophagous, saprophagous or generalists), body length (clypeus to pygidium, in millimetres), and habitat use (forest specialists, grassland specialists, habitat generalists or too rare to classify) (see Chazdon et al., 2011) (Supplementary material: Table S1). These attributes are widely used to identify the functional groups of dung beetle species and each one has a particular impact on the ecosystem functioning (Barragan et al., 2011; Nichols et al., 2013). We classified dung beetle species into functional groups according to food relocation behaviour following the literature (Halffter & Edmonds, 1982; Scholtz et al., 2009). Dung beetle body length was mostly obtained from the literature (Díaz & Favila, 2009; Howden & Gill, 1993; Howden & Young, 1981; Zunino & Halffter, 1997) because we were unable to calculate the length from the old material. For the species that we could calculate body length, we obtained this variable by measuring dung beetles with a digital calliper (to the nearest 0.01 mm), using 1 to 10 individuals per species, depending on number of

available individuals. We determined food preference for species with $n \geq 5$ recorded individuals following Halffter and Arellano (2002): species in which more than 80% of their individuals were collected in faeces or carrion were considered coprophagous or necrophagous, and species in which less than 80% of their individuals were collected in one of the resource types was classified as generalist. Furthermore, we used literature to determine food preference from species that were rarely recorded in this study ($n < 4$) (Bourg et al., 2016; Navarrete & Halffter, 2008). We classified species according to their habitat use using the Multinomial Classification Model (CLAM) proposed by Chazdon et al. (2011). This model uses the relative species abundances in 2 distinct habitat categories (i.e., forest fragments and pastures), thus minimizing potential biases attributable to differences in sampling intensities between the 2 habitat categories and insufficient sampling of rare species in each habitat (Chazdon et al., 2011). We applied the liberal threshold of habitat specialization (K or specialization threshold value to assign shared species as habitat specialists), using the “simple majority” rule, with a cut-off point $K = 1/2$, which is highly sensitive for determining the habitat specificity of a given species. This analysis was carried out using the CLAM software version 1.0 (Chao & Lin, 2011). This method allowed classification of species as forest specialists, pasture specialists or habitat generalists. Species with insufficient sampling were grouped as “too rare”.

Based on 4 dung beetle traits important for ecosystem functioning, we calculated the “trait distances” between species based on Gower distance coefficient using the function “gowdis” from the R package FD (Laliberté et al., 2014). We then ran a principal coordinates analysis (PCoA; based on the Gower distances between species) using the function “cmdscale” from the R package stats (R Core Team, 2021) to provide trait vectors for subsequent β -diversity partitioning analyses and functional richness calculation. Contrary to the original trait variables, these trait vectors are continuous variables that can be used to describe trait differences between species. In practice, Euclidean distances between species based on the first 4 PCoA axes and original Gower distances between species were very strongly correlated (Mantel $r = 0.943$, $p = 0.001$), indicating that the 4 trait vectors reproduce well the information in the original species-by-species trait distances (da Silva et al., 2018). Besides, the number of dimensions (i.e., PCoA axes) was chosen based on the quality of the functional space, i.e., the extent to which it accurately represents the initial functional distances between species pairs, quantified by the mean squared-

deviation index (Maire et al., 2015). We kept the minimum number of axes (i.e., 4 axes) that provides a high-quality functional space to minimize the number of sites or months we had to exclude to attain computation requirements (i.e., higher number of taxa than PCoA axes) (Villéger et al., 2008). Differences in quality between 4 and more dimensional spaces were relatively low, allowing us to construct a faithful representation of the initial functional trait values (Castro et al., 2020).

For each site per habitat type and period, we calculated dung beetle functional richness (FRic; amount of niche space occupied by the species within a community; Villéger et al. [2008]) and both taxonomic and functional β -diversity based on Sorensen dissimilarity. We calculated β -diversity using 2 approaches: “within year β -diversity” (between months for 1999-2000 and 2016-2017 separately) and “between year β -diversity” (between sampling periods of 1999-2000 and 2016-2017, after pooling the monthly data per period). We then partitioned β -diversity into its components of substitution and gain/loss (Legendre, 2014; Schmera et al., 2020) using the functions “beta.multi” (for taxonomic β -diversity) and “functional.beta.multi” (for functional β -diversity) from the R package BAT (Cardoso et al., 2020) and betapart (Baselga & Orme, 2012), respectively. These functions compute 3 multiple-time dissimilarities accounting for the substitution and the gain/loss components of taxonomic and functional β -diversity, and the sum of both values (Legendre, 2014; Schmera et al., 2020). The taxonomic partitioning is based on the species-by-site table (either species-by-forest sites or species-by-pasture sites), while the functional partitioning is based on the first 4 PCoA axes. We used different approaches to calculate taxonomic and functional β -diversity values and its components because the Podani’s approach is more robust to disentangle substitution and gain/loss of species than Baselga’s approach (Schmera et al., 2020). Podani’s approach calculates substitution and richness difference components and but not nestedness, which is more adequate for our data. On the other hand, Baselga’s approach is more robust than Podani’s approach to evaluate functional β -diversity metrics because it produces higher quality of functional spaces and functional substitution values independent of differences in functional richness (Loiseau et al., 2017). Therefore, we used Podani’s approach for the taxonomic calculations and Baselga’s approach for the functional calculations. Due to the low values of species richness found in most pasture sites (samples with < 5 species: 89.5% in 1999-2000 dataset, 73.7% in 2016-2017 dataset, 33.3% in between-years dataset; Supplementary material: Table S1, S2), we were unable to calculate functional values for most pasture sites because of computational

restrictions; this analysis does not run with $N > 2$ sites and if sites have fewer than 5 species (Baselga et al., 2018) (Supplementary material: Table S2). Therefore, we used functional values only for forest fragments (those with ≥ 5 species) in further analyses.

We used generalized linear models (GLMs) in the R software (R Core Team, 2021) to test the effect of habitat type (forest fragments and pasture), sampling year (1999-2000, 2016-2017, and ‘between-years’), and the interaction between habitat type and sampling year on the temporal patterns of taxonomic dung beetle β -diversity and its substitution and gain/loss components (i.e., Sorensen dissimilarity and its components of substitution and richness difference were the response variables). Using GLMs, we also tested the effect of sampling year on functional β -diversity and its substitution and gain/loss components of dung beetles inhabiting forest fragments only. The binomial distribution corrected for overdispersion (quasi-binomial) for total dissimilarity (Sorensen) and its components were used for both taxonomic and functional values after checking the data dispersion and the resulting residuals (Crawley, 2013).

Results

A total of 4,563 individuals of 43 species were sampled (Supplementary material: Table S1). We found that habitat type had an effect on taxonomic β -diversity and on its richness difference component when analysing dung beetles’ temporal β -diversity (Table 1). Pastures had a taxonomic β -diversity and its richness difference component respectively 1.42 and 1.56 times higher than forest fragments, regardless the sampling year (Fig. 1a, c). However, there was no effect of habitat type (forest fragments or pasture), sampling year, or their interaction on species replacement (Fig. 1b).

Regarding functional diversity, we found that pastures had a lower functional richness than forest fragments in both sampling periods, being 1.93 times lower in 1999-2000 and 1.69 times lower in 2016-2017 (Table 2, Fig. 2). We also found that sampling year had effect on temporal values of functional β -diversity of forest fragments (Table 2). Within-year values were higher than between-year values (Fig. 3). There was no difference in temporal values of the components of turnover and nestedness of functional β -diversity in forest fragments (Table 2).

Discussion

Here, we evaluated short- and long-term changes in dung beetle taxonomic and functional diversity in forest fragments and surrounding cattle pastures. According

Table 1

Results of generalized linear models estimating the effect of habitat (forest fragments or pasture), period (1999-2000, 2016-2017, and between sampling periods), and their interaction on dung beetles' taxonomic β -diversity (Sorensen dissimilarity) and its components of replacement and richness difference (Podani's approach). Temporal β -diversity values were calculated among months of each sampling period and between sampling periods. Sum Sq = sum of squares; Df = degrees of freedom; $p < 0.05$ are in bold.

Response variable	Predictor variable	Sum Sq	Df	F-value	<i>p</i>
Sorensen	Habitat	1.8244	1	17.6044	0.0001
	Period	0.2438	2	1.1764	0.3177
	Habitat: period	0.6414	2	3.0943	0.0551
	Residuals	4.6636	45		
Replacement	Habitat	0.3777	1	2.4295	0.1261
	Period	0.6018	2	1.9356	0.1562
	Habitat: period	0.1785	2	0.5742	0.5672
	Residuals	6.9955	45		
Richness difference	Habitat	0.7994	1	6.436	0.0147
	Period	0.2378	2	0.9572	0.3917
	Habitat: period	0.4816	2	1.9385	0.1557
	Residuals	5.5895	45		

Table 2

Results of generalized linear models estimating the effect of period (1999-2000, 2016-2017, and between sampling periods) on dung beetles' functional richness of the entire assemblage and functional β -diversity (Sorensen dissimilarity) and its components of substitution and nestedness (Baselga's approach) inhabiting forest fragments. Temporal β -diversity values were calculated over months of each sampling period and between sampling periods. We were unable to calculate functional metrics for pastures due to low site richness. Sum Sq = sum of squares; Df = degrees of freedom; $p < 0.05$ are in bold.

Response variable	Predictor variable	Sum Sq	Df	F-value	<i>p</i>
Functional richness	Habitat	1.7565	1	6.9908	0.0133
	Period	0.3614	1	1.4384	0.2405
	Habitat: period	0.0006	1	0.0022	0.9629
	Residuals	7.0352	28		
Sorensen	Period	1.8929	2	3.3632	0.0486
	Residuals	8.1609	29		
Substitution	Period	2.3620	2	2.7201	0.0827
	Residuals	12.5910	29		
Nestedness	Period	0.3466	2	0.5375	0.5899
	Residuals	9.3497	29		

to our first prediction, pastures suffered more important compositional changes than forest fragments over time, both within-years and between-years. The observed monthly changes in pastures were similar across sampling years and were explained by species gains/losses (richness

differences) through time. This result is explained by the low species richness and functional richness found in pastures when compared to neighbouring forest fragments. On the other hand, contrary to our second prediction, taxonomic β -diversity was not higher between sampling

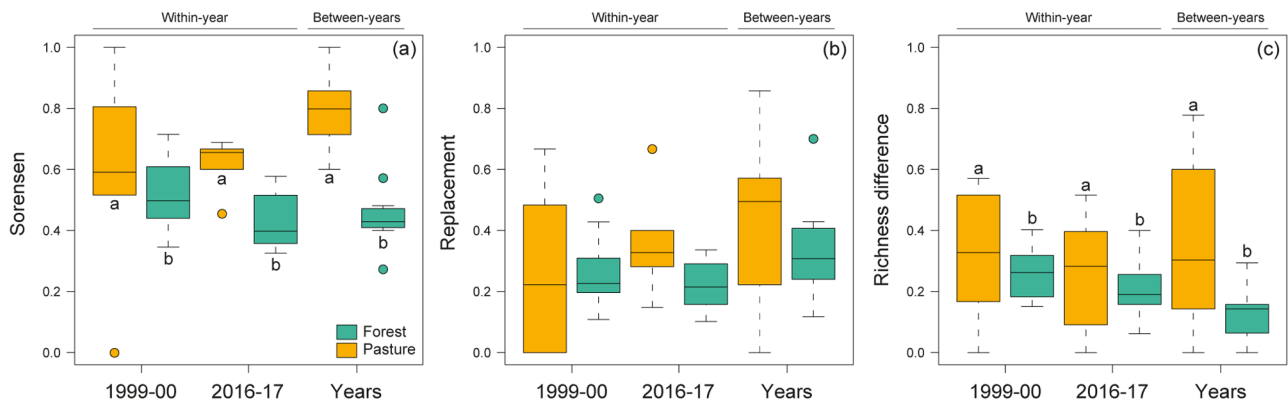


Figure 1. a) Dung beetle taxonomic β -diversity (Sorensen dissimilarity), b) its components of substitution, c) richness difference between months of 1999-2000 and 2016-2017 and between sampling periods (1999-2000 vs. 2016-2017) per habitat type (forest fragments = 11 sites; pasture = 6 sites). Circles represent outliers and different letters mean statistical differences.

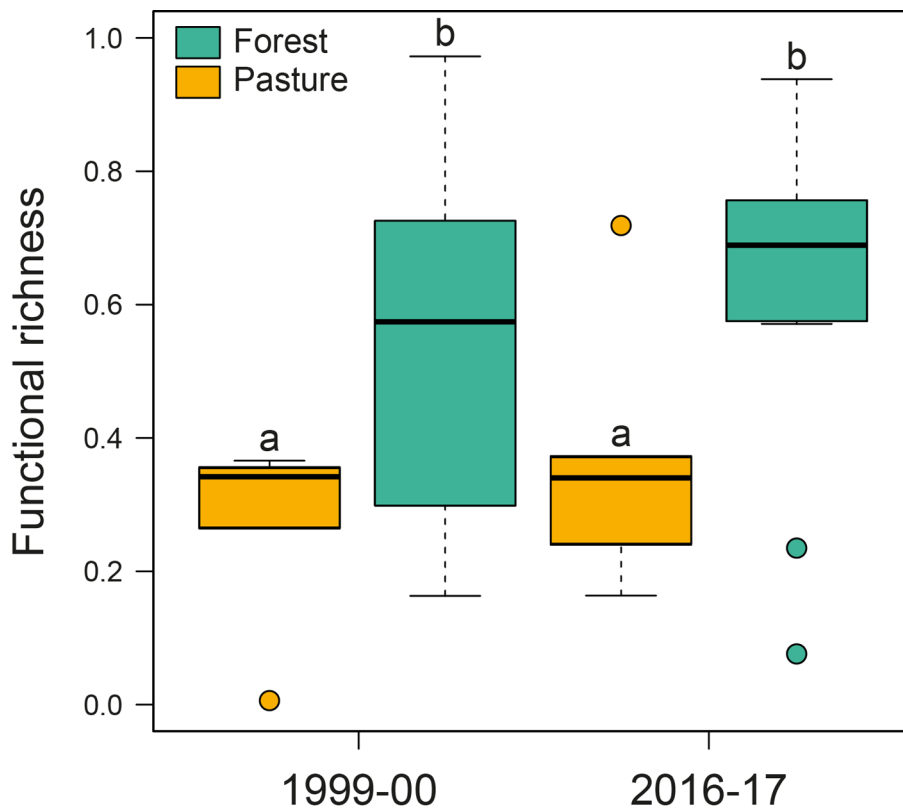


Figure 2. Dung beetle functional richness in forest fragments (n = 11) and pastures (n = 6) during sampling years of 1999-2000 and 2016-2017. Circles represent outliers and different letters mean statistical differences.

years than within years, despite there was a general gain of species from 1999-2000 to 2016-2017 (Salomão et al., 2020). Within-year functional β -diversity was higher than

between-years in forest fragments, although we were unable to evaluate this pattern for pastures. Also, contrary to our second prediction, dung beetle assemblages in forest

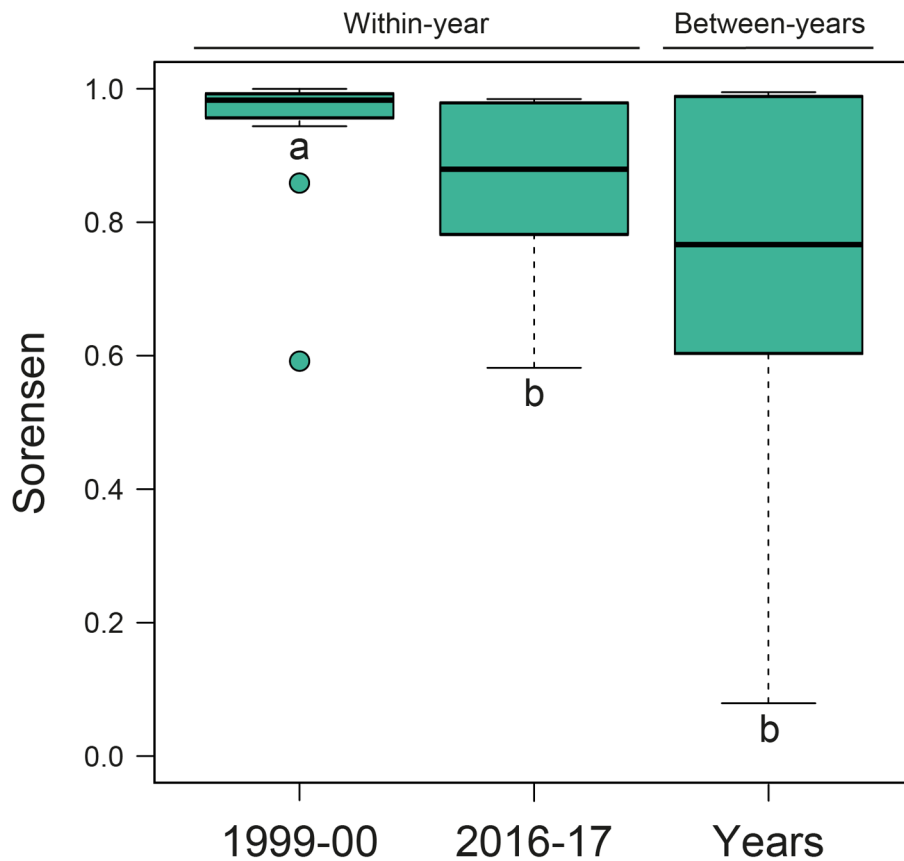


Figure 3. Dung beetle functional β -diversity (Sorensen dissimilarity) among months of 1999-2000 and 2016-2017 and between sampling years (1999-2000 vs. 2016-2017) of forest fragments ($n = 11$ sites). Circles represent outliers and different letters mean statistical differences. We were unable to calculate functional metrics for pastures due to low site richness.

fragments were more stable between-years than within-years, besides being functionally richer than pastures.

Pastures encompassed a higher taxonomic β -diversity of dung beetles than forest fragments at LTBR, which may be associated to the more unstable conditions of pastures and higher environmental complexity and stability of forest fragments (Filgueiras et al., 2019; Salomão et al., 2020). In open habitats, dung is exposed to high heat and desiccation rate, which implies in shorter periods of dung beetle activity on dung during the day (Horgan, 2005) and loss of attractiveness due to the creation of a hard dung crusts that reduce the scent emitted or are avoided by some species (Frank et al., 2018; Horgan, 2008). This can lead to a low reproductive success and decreased rates of dung decomposition (Horgan, 2005). Besides, extreme temperatures and higher temperature variation found in open habitats can cause physiological intolerance of dung beetle species to inhabit or constantly use these habitats (Giménez-Gómez et al., 2020). Pastures also have low

heterogeneity regarding resources and habitat structure compared to forest fragments, which provide a high diversity of food resources that can fulfil the nutritional requirements of different dung beetle species (Gill, 1991). Herbivorous dung is the dominant food resource in pastures and has intermediate to low nutritional values compared to carnivorous and omnivorous dung (Frank et al., 2017; Horgan, 2008). The diversity of food resources in forest fragments can enhance both taxonomic and functional diversity of dung beetles, which can show many specialized species (Larsen et al., 2006). Besides, both dung beetles and detritus-feeding flies use mammal dung, carrion, and decaying fruits for feeding and/or breeding (Hanski, 1991). When they occur, both carrion and decaying fruits can be rapidly consumed by flies and other insects in open habitats, reducing the colonization chance by dung beetles (Horgan, 2005, 2008). These pasture-associated conditions can make them a more dynamic environment in terms of dung beetle composition.

Neotropical pastures harbour less species richness and abundance than forest fragments (Braga et al., 2013; Escobar et al., 2007; Estrada et al., 1998; Horgan, 2008), and they have been acknowledged to have more spatially homogeneous dung beetle assemblages when compared to forest fragments (Escobar et al., 2007; Solar et al., 2015). Therefore, temporal changes in agricultural land-uses in LTBR over 17 years (i.e., long term effects) due to increased forest area, decrease of livestock activity, and change of vegetation successional stage in open habitats may have caused a higher compositional change in pastures than in forest fragments, represented by species gains/losses. Another possibility is the way in which the compositional change of assemblages over time has been evaluated, since the approaches to partition β -diversity into its components of replacement and gain/loss are relatively recent (Legendre, 2014). Noriega et al. (2021) also found a nested gain/loss component as primary driver of the temporal β -diversity of dung beetles across a long-term successional recovery of the Amazon Forest from human-induced disturbances. Forest fragments and pastures also have different dung beetle species compositions due to the distinct environmental requirements of these species (da Silva et al., 2019). For instance, *Canthidium centrale* (Boucomont, 1928), *Deltochilum pseudoparile* Paulian, 1938, *Canthidium* sp., *Uroxys bonetti* Pereira & Halffter, 1961, *Uroxys platypiga* (Howden & Young, 1981), *Dichotomius satanas* (Harold, 1867), *Canthidium pseudoperceptibile* Kohlmann & Solís, 2006, *Canthidium ardens* Bates, 1887, *Eurysternus maya* Génier, 2009, *Canthon subhyalinus* Harold, 1867, *Canthon morsei* Howden, 1966, *Canthon vazquezae* Martinez, Halffter & Halffter, 1964, *Coprophanaeus corytus* (Harold, 1863), *Bdelyopsis newtoni* Howden, 1971, *Canthon eurycelis* Bates, 1887, *Canthon femoralis* Chevrolat, 1834, *Deltochilum carrilloi* González-Alvarado & Vaz-de-Mello, 2014, *Onthophagus asperodorsatus* Howden & Gill, 1993, and *Onthophagus violeatae* Zunino & Halffter, 1997 were exclusively found in forest sites. *Canthon indigaceus chiapas* Robinson, 1948, *Canthidium pseudopuncticolle* Solís & Kohlmann, 2004, *Phanaeus tridens* Castelnau 1840, and *Phanaeus mexicanus* Harold, 1863 were found exclusively in pasture sites. Dung beetles are also affected by differences in climatic conditions during a year (Andresen & Feer, 2005; Ferreira et al., 2019; Neves et al., 2010), but forest fragments can buffer harsh climatic conditions both below and aboveground when compared to pastures (da Silva et al., 2019; Suggitt et al., 2011). This would lead to a high temporal microclimatic stability in forest fragments that allows different species to occur throughout the year, while species in pastures would be restricted to periods of more favourable conditions,

causing high compositional changes. Under this rationale, the high changes of environmental conditions and resource availability expected to occur in pastures over the short- and long-term may cause the observed high compositional changes of dung beetle assemblages in these habitats.

The high values of temporal taxonomic β -diversity found in pastures (both within-years and between-years) must be taken with caution. This pattern might have emerged because of the species- and individual-poor assemblages sampled in pastures (Salomão et al., 2020), which resulted in low functional richness in both sampling years when compared to forest fragments. The replacement or loss of few species in pastures can have a considerable impact on the estimates of temporal taxonomic β -diversity. Dominant functional groups, which can maintain a similar functional structure over space and time, may cause a pattern of low functional β -diversity despite being more taxonomically dissimilar (Villéger et al., 2012). In our case, although richer, forest fragments were dominated by both rollers and tunnellers, with gains of dwellers through time (Supplementary material: Table S1). On the other hand, the low species richness, plus the gain of dwellers, the spatial dynamic of rollers, and a positive balance between disappearing and new appearances of some tunnellers (Supplementary material: Table S1), probably caused a high taxonomic β -diversity in pastures between sampling years and within-years. We also expect that these factors would cause a high functional β -diversity in pastures over time, although we were unable to measure these patterns. Besides, our results may suggest that increased species richness observed in forest fragments does not necessarily result in temporal changes of functional diversity. Barragan et al. (2011) found that both fragments and continuous forest in Mexican Montes Azules Biosphere Reserve included more functionally redundant dung beetle species, while all the species found in pastures were functionally different, despite pastures having low species richness and functional richness. On the other hand, forest fragments harbour more redundant species and high functional richness that ensure the functioning of the ecosystem even with the loss of some species with similar functions (Rosenfeld, 2002). In a meta-analysis, Biggs et al. (2020) showed that functional redundancy is correlated with ecological resilience and stability of communities and ecosystems, as ecosystem function of communities with more redundant species is buffered against the loss of individual species.

As a whole, the deforestation of primary and secondary forests to expand agricultural area decreased in Mexico from 1980 to 2000 (Gibbs et al., 2010) and stabilized to ca. 500,000 ha loss per year between 1993 and 2007 (Rosete-Vergés et al., 2014). In Mexico, there are few studies at the national level to understand the processes of

change in land-use and vegetation. Nonetheless, at local and regional scales, there is a trend of forest loss and increase of agriculture and human settlements (Monjardín-Armenta et al., 2017). Besides, there are currently 182 protected natural areas in Mexico, covering 90.8 million hectares in total (Conanp, 2019). The establishment of the LTBR has led to the recovery of native vegetation, involving the increase of forested area and the reduction of the agricultural matrix (Vega-Vela et al., 2018). In the LTBR, there have been gains of dung beetle species and we are able to show that dung beetle assemblages are more stable in forest fragments than in pastures (Salomão et al., 2020). However, this recovering process can be slower than we expect in other regions (Audino et al., 2014; Escobar et al., 2008). For instance, Audino et al. (2014) found that 18 years since active restoration has not been long enough to recover a stable and diverse dung beetle assemblage in sites of the Atlantic Forest. Factors such as habitat loss in the surrounding landscape and increasing isolation of sites can contribute to the temporal changes of dung beetle assemblages (Escobar et al., 2008). In this sense, long-term studies in different ecosystems would be highly informative, as they are useful to inform about conservation success or failure and ways to carry out better management practices that should take into account integrative approaches at landscape-to-regional scales (Halffter, 2005).

In general, Neotropical pastures have lower taxonomic and functional diversity of dung beetles than adjacent forest fragments (Barragan et al., 2011; da Silva et al., 2019; Horgan, 2008; Solar et al., 2015). Removal and burial of dung and seeds are also higher in forest fragments than in pastures, which is associated to dung beetle richness, abundance, and biomass (Andresen, 2003; Horgan, 2005). Losses of dung beetle species or functional groups could leave unsaturated niche spaces or be replaced by other organisms, such as flies and termites in open habitats (Herrick & Lal, 1996; Horgan, 2008). On the other hand, these species- and individual-poor assemblages found in pastures of the LTBR are important to provide their ecosystem functions, even in a reduced way. For instance, dung beetles can reduce the survival and availability of gastrointestinal parasites in pastures, besides their essential role in dung degradation and nutrient cycling (Sands & Wall, 2017). However, they can be severely impacted by the common use of pesticides in livestock systems that disrupt their life cycle and behaviour (Alvarado et al., 2018; Correa et al., 2022; Verdú et al., 2018). This issue is particularly important considering the low taxonomic and functional richness estimates found in pasture sites.

Considering the general gain of species over the 17 years (Salomão et al., 2020), forest fragments have

been maintaining and accumulating their taxonomic and functional diversity, suggesting a coupled conservation and recovery of dung beetle assemblages in the LTBR. Pastures harbour poor dung beetle assemblages with high temporal dynamics both within-years and between-years spaced 17 years apart. We showed that using taxonomic and functional approaches, interpreted in the light of accurate biological responses as we have shown for temporal patterns of taxonomic diversity of dung beetles, can be a suitable way for the long-term evaluation of biodiversity patterns. Evaluating short- and long-term changes of biological communities intrinsically related to ecosystem processes of forest regeneration, such as dung beetles, can be considered as an important tool to better inform society and decision-makers regarding effective conservation of biodiversity and ecosystem functioning in protected areas.

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