



Structure of dung beetle assemblages (Coleoptera: Scarabaeidae: Scarabaeinae) in native forest and exotic pastures in the Southwest of the Brazilian Amazon

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Received: 13 June 2023 / Accepted: 14 December 2023 / Published online: 3 January 2024

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Abstract

The implementation of exotic pastures is responsible for significant deforestation in the Amazon rainforest. The pasturelands in the Amazon are created through both legal and illegal means, and are responsible for major biodiversity loss. In this study, we evaluated the effect of an anthropogenic habitat type (i.e., exotic pasture) on native dung beetle assemblages (Coleoptera: Scarabaeidae: Scarabaeinae) – an excellent bioindicator group for measuring biodiversity-loss. We analyzed dung beetle diversity and assemblage structure in a large and well-conserved forest fragment and in an exotic pasture (*Urochloa brizantha* cv. Marandu; Poaceae) that is used for cattle-ranching activities, both located in the Southwestern Brazilian Amazon. A total of 569 individuals belonging to nine genera and 31 species of dung beetles were collected. From the sampled species, 13 were collected in both habitats, 16 species were exclusive to the native forest, and only two were found exclusively in the exotic pasture. Species richness as a whole and specifically of paracoprid dung beetles was higher in the forest fragment. Our findings also revealed a distinct assemblage structure between native forest and exotic pasture. In conclusion, our results provide evidence that the dung beetle assemblage in exotic pasture is a subset of the assemblage present in native forest, with a poor richness of species, indicating that dung beetles are drastically affected by the opening of new areas for implementation and expansion of pasturelands in the Amazon.

Keywords Agropastoral systems · Amazon rainforest · Bioindicators · Coprophagous beetles · Tropical forests

Introduction

Tropical ecosystems feature as one of the most discussed regions in the world with regards to current novel conservation strategies because although they harbour a high species

diversity, they are also one of the most threatened ecosystems (Myers et al. 2000; Hoang and Kanemoto 2021). There have been public and private initiatives aiming to understand and mitigate the effects of converting natural landscapes into anthropogenic ones (Melo et al. 2014; Erbaugh et al. 2019;

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Drummond et al. 2021). Through the assessment of biodiversity in tropical ecosystems, and their response towards different disturbance regimes, conservation ecologists aim to understand the levels of tolerance of the ecological communities to these novel and challenging systems that have been occurring during the Anthropocene (e.g., Garcia-Moreno et al. 2014; Martínez-Ramos et al. 2016; Erbaugh et al. 2019). Although there is a clear unidirectional response (i.e., anthropogenic landscapes impoverish tropical biodiversity, see Gardner et al. 2009), it is crucial to understand the reasons behind the success of some biological groups in the disturbed environments. In addition, by analyzing how ecological communities and their particular subsets respond to habitat transformation, we may predict the outcomes of novel future scenarios triggered by human activities.

The Amazon is a continental biome that occupies almost the entire Midwest of South America, and is the main source of Neotropical biodiversity, as well as one of Earth's greatest biological treasures, providing crucial ecosystem goods and services to humanity (e.g., Myers 1997; Foley et al. 2007; Antonelli et al. 2018). However, despite its invaluable ecological and economic importance, the Amazon rainforest has been drastically deforested in recent years (e.g., Matricardi et al. 2020; Stropp et al. 2020; Lapola et al. 2023). One of the current main threats to the Amazon rainforest is from cattle-ranching activities, which comprises the conversion of native vegetation into exotic pastures (Neate-Clegg and Şekercioğlu 2020; Paiva et al. 2020). From the introduced pasturelands in the Amazon, one of the grass species most commonly used is the African *Urochloa* spp. (Syn. *Brachiaria*) (Rao et al. 1996; Galdino et al. 2016; IBGE 2017). Exotic pasture implementation is responsible for a significant rise in deforestation in the Amazon. The deforestation stems from the center of South America towards the north of the continent, which results in the presently termed `Amazonian arc of deforestation` (Durieux et al. 2003; Cavalcante et al. 2019). As a consequence of this novel Amazonian landscape, biodiversity in this biome is facing a challenging scenario, encompassing habitats markedly different from the native ones. The implementation and expansion of pasturelands in the Amazon, which comes from legal and illegal means, causes drastic negative impacts on its biodiversity and physical structure (Pereira et al. 2000; Fearnside 2002; Makewitz et al. 2004).

Over the last decade, dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) have gained a notable importance as a bio-monitoring group in tropical anthropogenic landscapes (Gardner et al. 2008; Scholtz et al. 2009; Silva et al. 2017). Abiotic and biotic factors, such as climate and mammal presence, are intrinsically linked to dung beetle diversity (e.g., Davis et al. 2002; Scholtz et al. 2009). Shifts in environmental conditions tend to directly change dung beetle species composition and

assemblage structure (e.g., Silva et al. 2014, 2017), allowing the assessment of finer nuances in the effects of habitat change on biodiversity. Thus, the dung beetles show direct responses to anthropogenic activities, such as deforestation and the alteration of native habitats (e.g., Halffter et al. 1992; Halffter and Favila 1993; Louzada et al. 2010; França et al. 2016; Silva et al. 2017; Correa et al. 2020). Moreover, in dung beetle communities, each functional group interacts with the environment in a particular manner, presenting single responses towards recent habitat transformations in the tropics (e.g., Salomão et al. 2019; Correa et al. 2020).

Previous studies indicate that the conversion of Amazon native forests into pastures are harmful for dung beetle diversity (e.g., Klein 1989; Quintero and Roslin 2005; Scheffler 2005; Quintero and Halffter 2009; Silva et al. 2016, 2017). Nonetheless, these studies are regional and large portions of the Amazon biome lack studies of this process, such as the Southwest of Brazilian Amazon (state of Rondônia), in which so far only one study focused on assessing such dynamics (Silva et al. 2014). The Southwest Brazilian Amazon has an important role regarding the dynamics of conversion of native forests into exotic pastures, since it is located exactly in the ecotone that comprises the Amazonian arc of deforestation. In this study, we evaluated the effect of the anthropogenic habitat type (i.e., exotic pasture) on native dung beetle assemblages. In order to analyze the effect of land use change, we studied dung beetles from a large and well-conserved forest fragment, as well as from an exotic pasture that is used for cattle-ranching activities. More specifically, we analyzed the whole dung beetle assemblages (dung beetle diversity and assemblage structure), as well as each functional group separately. By analyzing ecological responses under these two perspectives, we may attain a more complete and detailed scenario regarding groups of dung beetles that are most affected by habitat types.

Materials and methods

Study sites

This study was carried out in the municipality of Itapuã do Oeste, state of Rondônia, Northern Brazil (09°18' S, 63°11' W; elevation of 119 m) (Fig. 1). This region is located in the Southwestern Amazon region, with a characteristic ombrophilous dense forest that is typical of the Amazon biome (IBGE 2006). According to the Köppen classification system, the climate of the study region is Am, tropical wet (tropical monsoon climate) (Alvares et al. 2014). The dry season corresponds to the months of June, July and August (mean monthly rainfall: 31.8 mm), while the other months comprise the rainy season, with 229.5 mm of mean monthly rainfall (Tejas et al. 2012). The region has an average annual temperature of 26.9 °C (ranging from 20.9 to 33.8 °C) and

average annual precipitation of 2,161 mm (ranging from 1,592 to 2,670 mm) (Tejas et al. 2012).

The landscape of the study area is representative of the current drastic Amazon transformation due to agricultural practices being located in the transition between the conserved portion of the ecosystem and the arc of deforestation between Amazon and Cerrado biomes (Fig. 1). Northernmost of the study area, the continuous Amazon forest occurs, while the Itapuã do Oeste municipality surroundings and its southernmost portion comprise a mosaic of forest fragments and agricultural matrix (Fig. 1). This mosaic is located near on the banks of the Jamari River, being surrounded by fragments of the Amazon rainforest and extensive exotic pastures for livestock (Fig. 1).

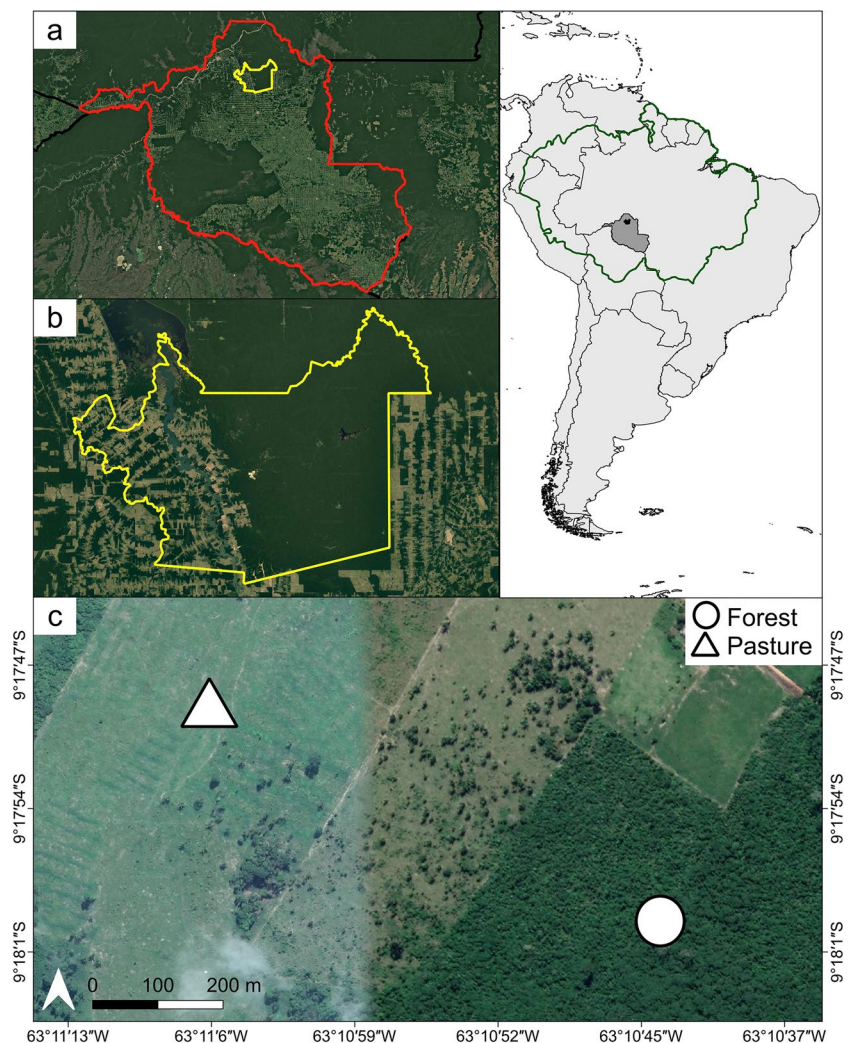
This study was performed in the two most representative, and contrasting, habitat types of the region:

- 1) Amazon forest fragment (*terra firme* vegetation) which is ca. 120 ha in size. This fragment comprises a primary forest with low levels of anthropogenic activity, such as

selective logging and extraction of native fruits (Brazil nuts – *Bertholletia excelsa* Humb. & Bonpl.; Lecythidaceae and açai – *Euterpe oleracea* Mart.; Arecaceae). Plant species are dominated by the families Arecaceae, Melastomataceae, Fabaceae, Lauraceae, Lecythidaceae, and Meliaceae. Studies conducted in forest fragments in the state of Rondônia indicate the presence of medium and large-sized mammals, such as jaguar (*Panthera onca* (L., 1758); Felidae), giant anteaters (*Myrmecophaga tridactyla* L. 1758; Myrmecophagidae), the nine-banded armadillo (*Dasybus novemcinctus* (L., 1758); Dasypodidae), and marmosets (*Leontocebus* spp.; Cebidae) (Medeiro et al. 2019; Silva et al. 2021), meaning these are the species to be expected to inhabit the study region. The studied forest fragment is ca. 6 km away from the neighboring continuous Amazon forest (Fig. 1);

- 2) A 30-ha exotic pasture composed of the grass *Urochloa brizantha* (syn. *Brachiaria brizantha*) cv. Marandu (Poaceae), which was introduced 16 years ago and is constantly used for cattle ranching activities (1.7 cattle-ha⁻¹).

Fig. 1 Geographic location of the study area. The state of Rondônia located in the Southwest of the Brazilian Amazon (a); the municipality of Itapuã do Oeste located to the North-east of the state of Rondônia (b); and the sampling sites: Amazon forest fragment (*terra firme* vegetation), and exotic pasture (*Urochloa brizantha* cv. Marandu; Poaceae) (c)



This pasture is subdivided in five plots of 6 ha each with a rotational grazing management structure. In such management regimes, the cattle remains between five and seven days in each plot, returning after a period between 25 and 35 days. In order to control cattle endo- and ectoparasites, synthetic veterinary products (mostly abamectin, doramectin, and ivermectin) are used readily in the livestock of the studied pasture, as well as in neighboring ones. The surroundings of this pasture are composed of a mosaic of agricultural crops, forest fragments, and other pastures (Fig. 1). This anthropogenic landscape was established about ca. 50 years ago in the study region.

Experimental protocol and dung beetle trapping

In the center of each habitat type (native forest and exotic pasture), five linear transects of 400 m were established, 200 m apart from each other. In each transect, four sampling units were established, each one 100 m apart from the others (see Larsen and Forsyth 2005; da Silva and Hernández 2015). We performed a Mantel test to investigate a possible spatial autocorrelation between sampling units and the dung beetle assemblages (see Moctezuma 2021), using the ‘vegan’ package in the R software version 4.2.1 (R Core Team 2023). Because we found a spatial autocorrelation ($r=0.54$; $p<0.01$), our sampling units should be treated herein as being pseudoreplicates. In each sampling unit, we installed two pitfall traps (2 m apart from each other), one baited with ca. 40 g of fresh pig dung and the other baited with ca. 40 g of carrion (decaying bovine meat). We used traps baited with different bait types in order to ensure an accurate representation of the local dung beetle functional and trophic groups (see Correa et al. 2016, 2023). This sampling method has been successfully used in ecological studies comprising tropical dung beetles (e.g., Ferreira et al. 2020; Correa et al. 2021a). To avoid any bias caused by seasonality on dung beetle assemblages (see seasonality in da Silva et al. 2013; Correa et al. 2021b; Araújo et al. 2022) we repeated this sampling across three months (December 2018, January and August 2019), representative of the different periods of the year. In total, this study encompasses a sampling effort of 20 spatial replicates per habitat type and 240 pitfalls installed (i.e., 20 replicates \times 2 traps \times 2 habitats \times 3 months).

Pitfall traps consisted of 15 cm diameter \times 9 cm height-plastic pots, which were buried at soil surface. Each trap was filled with a ca. 300 mL-solution of salt (30 g) and detergent (6 mL) to capture and preserve the collected specimens. The baits were placed in small plastic cups (50 mL) at the center of each trap using a wire as a bait holder. To avoid bait desiccation and damaging of the traps by leaf litter and rainfall, a plastic lid was inserted in the top of each pitfall trap. Traps were removed 48 h after their installation in the field. Collected specimens were kept in plastic bags with ethanol 70% for preservation until dung beetle sorting and taxonomic identification.

Taxonomic treatments

After the sorting of all collected material, the dung beetle specimens were identified to the genus level (Vaz-de-Mello et al. 2011) and then sent to the Universidade Federal de Mato Grosso (UFMT; Cuiabá, Mato Grosso, Brazil). At UFMT, dung beetles were identified to species level by two of the authors (i.e., CMAC and FZVM). Voucher specimens are deposited in the Entomological Section of the Zoological Collection at the UFMT (CEMT).

Data analysis

Inventory completeness was evaluated using a sample coverage analysis (see Chao et al. 2014; Hsieh et al. 2016), which comprises an individual-based approach. This analysis ensures that our sampling adequately represented the dung beetle assemblages of the native forest and exotic pasture studied herein. Sample coverage was performed using the R package iNEXT (Hsieh et al. 2016), in R software version 4.2.1 (R Core Team 2023). In addition, we plotted species rank-abundance distributions to visually compare patterns of species dominance in the two studied habitats.

To estimate dung beetle diversity in native forest and exotic pasture, we used the Hill numbers’ approach to calculate species richness (0D), exponential of Shannon diversity (1D) and the inverse of Simpson (2D), using the R package iNEXT (Hsieh et al. 2016). 0D is equivalent to species richness and is not sensitive to the species abundance (Jost 2006); 1D accounts for the most common species in a community (Jost 2006); and 2D accounts for the dominant species, giving more weight to them compared to 0D and 1D and being impervious to rare species (Jost 2006; Chao et al. 2014). Hill numbers are widely used in ecological studies (Chao et al. 2020). In this study, Hill numbers were calculated for the whole dung beetle assemblages and each functional group, according to their resource removal strategies (i.e., endocoprids, paracoprids and telecoprids; as proposed by Tonelli 2021). To compare dung beetle diversities between native forest and exotic pasture, $\pm 95\%$ confidence intervals were used (Hsieh et al. 2016).

To verify differences of assemblage structure between native forest and exotic pasture sites, we used Permutational Multivariate Anova (PERMANOVA; $p<0.05$), with 999 permutations (Anderson 2001). To test heterogeneity of multivariate dispersions between native forest and exotic pasture sites, we used Permutational Multivariate Analysis of Dispersion (PERMDISP; $p<0.05$) (Anderson 2001). To graphically represent the changes in dung beetle assemblage structure between native forest and exotic pasture sites, we used a Non-Metric Multidimensional Scaling analysis (NMDS) with 999 random restarts (Anderson and Willis 2003). PERMANOVA, PERMDISP and NMDS analyses were performed based on

Bray–Curtis dissimilarity matrix, and data of species abundance were standardized and square root transformed. All these statistical approaches were run in the Primer software version 6 with PERMANOVA+ (Clarke and Gorley 2006).

Results

We collected 569 individuals belonging to 31 species in nine genera of dung beetles. *Ateuchus* Weber, 1801 and *Canthidium* Erichson, 1847 were the most diverse genera ($S=7$ species in each genus), while *Deltochilum* Eschscholtz, 1822, *Pseudocanthon* Bates, 1887, *Coprophanaeus* Olsoufieff, 1924, and *Phanaeus* Macleay, 1819 were the least diverse

genera ($S=1$) (Table 1). In the native forest, we captured 29 species ($n=496$), whereas in exotic pasture, we collected 15 species ($n=73$) (Table 1). From the total species collected, 13 species were found in both habitats, 16 species were found exclusively in native forest, and only two species (namely *Canthon* sp. and *Pseudocanthon xanthurus* (Blanchard, 1846)) were found exclusively in exotic pasture (Table 1). The sample coverage estimator revealed a high sampling efficiency, ranging from 98% in native forest to 90% in exotic pasture (Table 1), indicating that the dung beetle survey representatively captured the true diversity of the local assemblage.

We found a higher number of species (0D) and abundant species (1D) in native forest compared to exotic pasture (Fig. 2a, b). Nonetheless, the number of dominant species

Table 1 Abundance, species richness, sample coverage, and functional groups of dung beetles collected in native forest and exotic pasture in Itapuã do Oeste, state of Rondônia, Southwest of the Brazilian Amazon. *Reported for the first time for the state of Rondônia, Northern Brazil (for a list of dung beetle species reported for the state of Rondônia, see Silva et al. 2022; Silveira et al. 2023)

Taxon	Forest	Pasture	Total	Funcional Group
<i>Ateuchus aeneomicans</i> (Harold, 1868)	13		13	Paracoprid
<i>Ateuchus substriatus</i> (Harold, 1868)	27		27	Paracoprid
<i>Ateuchus</i> sp. 1	2		2	Paracoprid
<i>Ateuchus</i> sp. 2	1	1	2	Paracoprid
<i>Ateuchus</i> sp. 3	11	3	14	Paracoprid
<i>Ateuchus</i> sp. 4	11		11	Paracoprid
<i>Ateuchus</i> sp. 5	1		1	Paracoprid
<i>Canthidium</i> aff. <i>barbacenicum</i> Preudhomme de Borre, 1886	3		3	Paracoprid
<i>Canthidium</i> aff. <i>dohrni</i> Harold, 1867	8		8	Paracoprid
<i>Canthidium</i> aff. <i>lentum</i> Erichson, 1847	3	1	4	Paracoprid
<i>Canthidium</i> aff. <i>melanocephalum</i> (Olivier, 1789)	1	1	2	Paracoprid
<i>Canthidium</i> sp. 1	32	3	35	Paracoprid
<i>Canthidium</i> sp. 2	20		20	Paracoprid
<i>Canthidium</i> sp. 3	7		7	Paracoprid
<i>Canthon conformis</i> Harold, 1868	5	6	11	Telecoprid
<i>Canthon histrio</i> (Lepeletier & Serville, 1828)	5	8	13	Telecoprid
<i>Canthon</i> aff. <i>simulans</i> (Martínez, 1950)	6	25	31	Telecoprid
<i>Canthon xanthopus</i> Blanchard, 1846*	2		2	Telecoprid
<i>Canthon</i> sp.		1	1	Telecoprid
<i>Coprophanaeus lancifer</i> (Linnaeus, 1767)	9		9	Paracoprid
<i>Deltochilum</i> sp.	27	1	28	Telecoprid
<i>Dichotomius</i> aff. <i>batesi</i> (Harold, 1869)	48	10	58	Paracoprid
<i>Dichotomius</i> aff. <i>lucasi</i> (Harold, 1869)	8		8	Paracoprid
<i>Dichotomius mamillatus</i> (Felsche, 1901)	1		1	Paracoprid
<i>Dichotomius worontzowi</i> (Pereira, 1942)	3		3	Paracoprid
<i>Eurysternus arnaudí</i> Génier, 2009	162	1	163	Endocoprid
<i>Eurysternus atrosericus</i> Génier, 2009	62	1	63	Endocoprid
<i>Eurysternus caribaeus</i> (Herbst, 1789)	15	3	18	Endocoprid
<i>Eurysternus wittmerorum</i> Martínez, 1988	2		2	Endocoprid
<i>Phanaeus chalconelas</i> (Perty, 1830)	1		1	Paracoprid
<i>Pseudocanthon xanthurus</i> (Blanchard, 1846)		8	8	Telecoprid
Number of individuals (Abundance)	496	73	569	
Number of species (Richness)	29	15		
Sample coverage (%)	98	90		

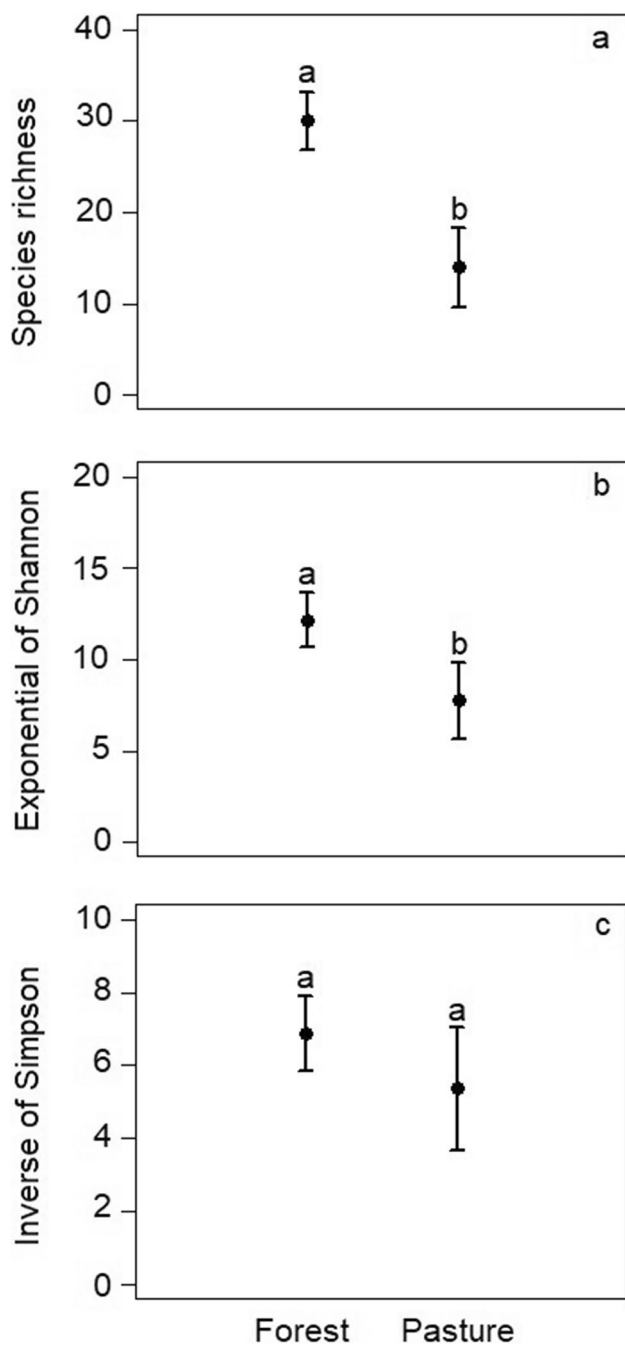


Fig. 2 Diversity numbers presenting mean species richness (a), exponential of Shannon entropy (b), and inverse of Simpson (c) of dung beetles sampled from native forest and exotic pasture in Itapuã do Oeste, state of Rondônia, Southwest of the Brazilian Amazon. Different letters indicate significant differences ($\pm 95\%$ confidence intervals)

(2D) did not differ between the two studied habitats (Fig. 2c). When analyzing diversity separated by functional groups according to resource removal strategy, the effects of habitat type on dung beetle diversity varied depending on the group analyzed (Fig. 3). For paracoprid dung beetles, native forest

presented higher diversity (0D , 1D , and 2D) than exotic pasture (Fig. 3). For endocoprid and telecoprid dung beetles, native forest and exotic pasture harbored similar diversities (Fig. 3).

From the total individuals collected in the native forest, the three most abundant species were *Eurysternus arnaudi* Génier, 2009 (32.7%), *Eurysternus atrosericus* Génier, 2009 (12.5%) and *Dichotomius* aff. *batesi* (Harold, 1869) (9.7%) (Fig. 4). In the exotic pasture, the most abundant species were *Canthon* aff. *simulans* (Martínez, 1950) (34.2%), *D.* aff. *batesi* (13.7%), *Canthon histrio* (LePeletier & Serville, 1828) (11.0%), and *Pseudocanthon xanthurus* (Blanchard, 1846) (11.0%) (Fig. 4). Eight of the species recorded in native forest (28% of the forest species) were rare (i.e., singleton or doubleton), whilst seven species were considered rare in exotic pastures (47% of the pasture species). Interestingly, two of the eight rare species observed in the native forest habitat (namely *Ateuchus* sp. 1 and *Canthidium* aff. *melanocephalum* (Olivier, 1789)) are also rare in exotic pasture, and the other six species are absent from exotic pasture. In this habitat type, three of the seven rare species are abundantly found in native forest (*E. arnaudi*, *E. atrosericus* and *Deltochilum* sp.).

The NMDS analysis organized sites into distinct groups, corresponding to the two types of habitats (Fig. 5), with assemblage structure differing significantly between native ecosystem (forest) and the introduced one (pasture) (PERMANOVA, Pseudo-F = 7.30, $p < 0.01$). Habitat types showed differences in the multivariate dispersion of points (PERMDISP, $F = 9.53$, $p = 0.01$), where exotic pasture had the highest dispersion value (*Native Forest* = 20.69 ± 1.46 ; *Exotic Pasture* = 42.76 ± 6.99).

Discussion

In the tropical ecosystems of America, the expansion of cattle ranching activity has led to alarming landscape transformation, which has been boosted since the second half of the twentieth century (Goodman and Hall 1990; Guevara et al. 2000; Pendrill et al. 2019). The Amazon region has a particular context regarding the expansion of cattle ranching activities: the conversion of conserved forest to pasture is relatively recent and has been a crucial debate topic in South American conservation policies (Goodman and Hall 1990; França et al. 2021). According to our results, the pasture habitats established in the Amazon rainforest has drastic negative consequences for biodiversity, since dung beetle diversity was markedly lower in pastures compared to forest habitat and assemblage structure was found to be completely distinct between native forest and the exotic pasture. Furthermore, the effect of habitat type on diversity depends on the functional group analyzed, suggesting that the effects of habitat transformation on diversity of dung beetles is group

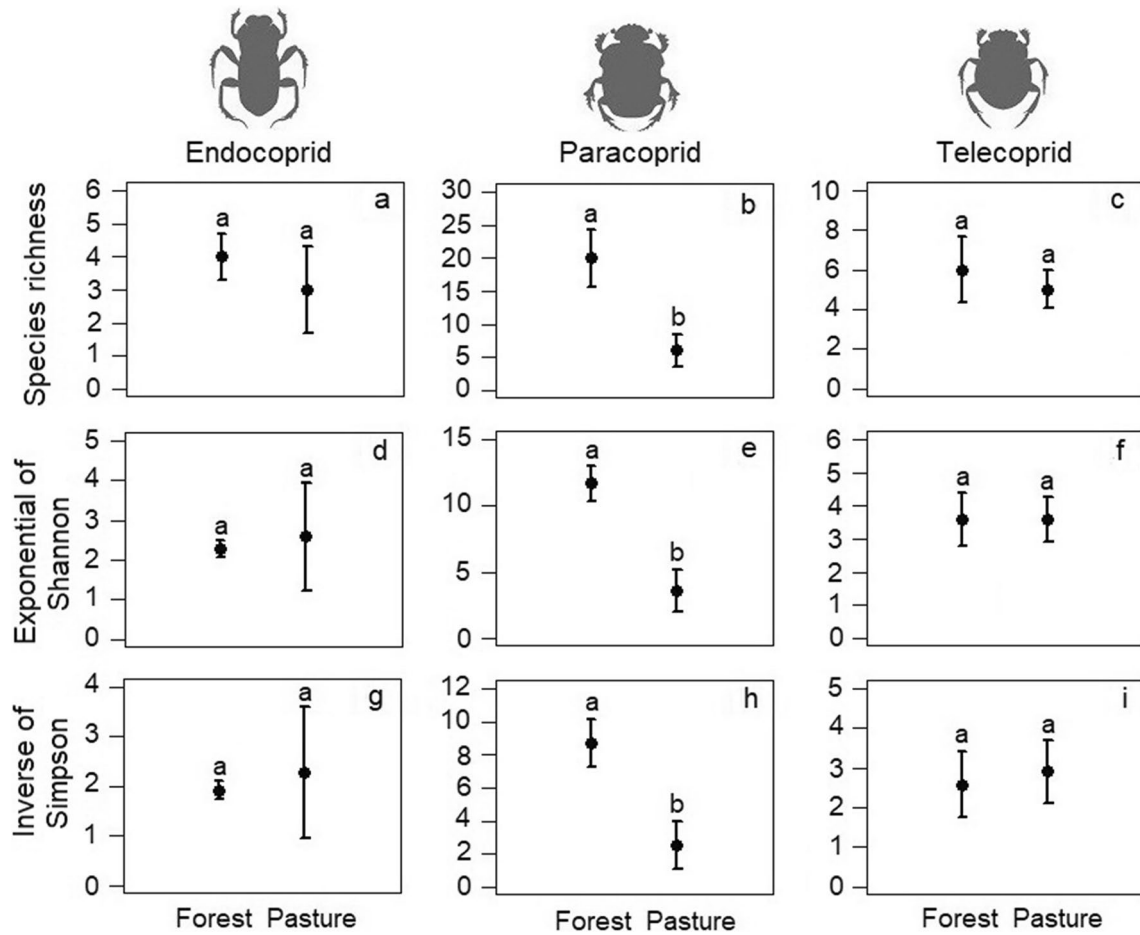
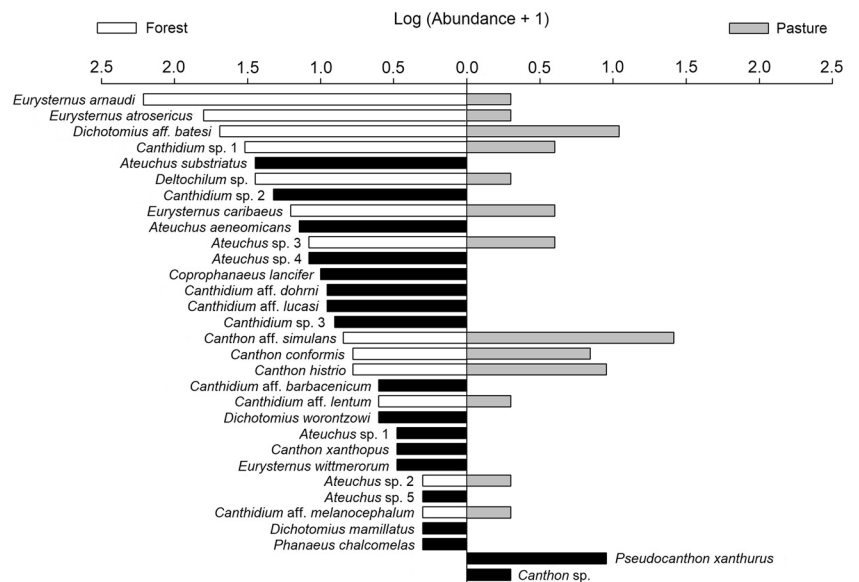


Fig. 3 Diversity numbers presenting mean species richness (a–c), exponential of Shannon entropy (d–f), and inverse of Simpson (g–i) of dung beetle functional groups separated according to their resource removal strategies (endocoprid, paracoprid and telecoprid), which

were sampled from the native forest and exotic pasture in Itapuã do Oeste, state of Rondônia, Southwest of the Brazilian Amazon. Different letters indicate significant differences ($\pm 95\%$ confidence intervals)

Fig. 4 Rank-abundance distribution in log (X + 1) of dung beetle species sampled in the Amazon forest (white bar) and exotic pasture (grey bar), in Itapuã do Oeste, state of Rondônia, Southwest of the Brazilian Amazon. Black bars represent exclusive species of each habitat type



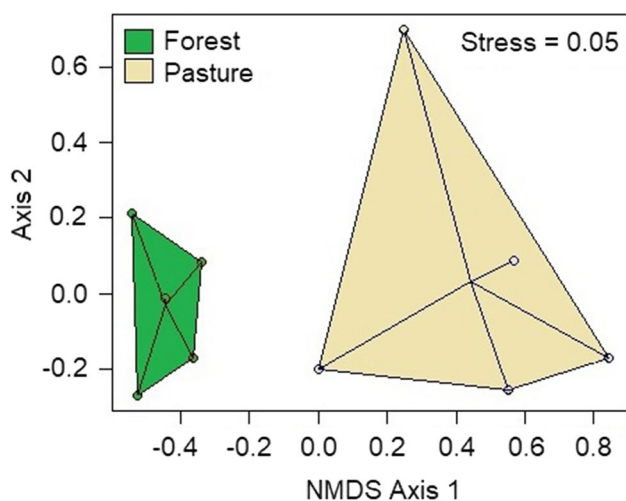


Fig. 5 Distribution patterns (NMDS) of the sampling points comparing assemblage structure (Bray–Curtis dissimilarity) of dung beetles between native forest and exotic pasture, and dispersion of points to centroid (lines), in Itapuã do Oeste, state of Rondônia, Southwest of the Brazilian Amazon

dependent. Such results reinforce the trend of biodiversity decline due to anthropogenic activities in tropical American landscapes.

The conversion of tropical forests into pastures generates abrupt shifts in environmental conditions (e.g., canopy cover, temperature, soil physical and chemical properties; Reiners et al. 1994; Pedrinho et al. 2018; Oliveira and Schmidt 2019), which are determinant for species establishment. Different from other forested ecosystems, in which there are species that clearly benefits from the open environments (higher temperatures, more sunlight) (Urbina-Cardona et al. 2006; Martínez-Falcón et al. 2018; Conover et al. 2019), we found that Amazon forests harbor dung beetle structures markedly distinct from those that inhabit neighboring pastures, in which dung beetle assemblages are a subset of those observed in forest. Most of the species that were recorded in the exotic pasture were less abundant than equivalent populations recorded in forests. The spatial distribution and abundances of species in each environment type represents a proxy of their habitat affinity (McGeoch et al. 2002). Thus, our results may allow us to propose two hypotheses: (1) dung beetles are using the pasture to move between forest fragments, rarely occurring in open areas; and (2) open areas maintain subsets of dung beetle populations. Both hypotheses are plausible and have been observed in other ecosystems. For example, in the *Deltochilum* and *Dichotomius* Hope, 1838 genera, there are species that use non-native habitats (e.g., pastures) to move across forested ecosystems (Cultid-Medina et al. 2015; Barretto et al. 2021), thus being more often observed in forest than in pastures. In addition, *Canthon cyanellus* LeConte, 1859 comprises of populations that segregate among different

habitat types (forests, pastures, live fences) according to their sex, maturation stage, and age (Salomão et al. 2021). As species traits play an important role on dung beetles' spatial distribution, diurnal activity of dung beetles could drive species movement across landscapes. For example, considering the crepuscular/nocturnal activity of *Dichotomius* species (Iannuzzi et al. 2016), such beetles could move between forest fragments during the periods in which pastures have cooler temperatures. Our results and previous data support the idea that Amazonian pastures are highly hostile environments for dung beetle diversity of the region (e.g., Silva et al. 2017). Apparently, only two species (namely *C. aff. simulans* and *P. xanthurus*), which are broadly distributed in different ecosystems and prefer open habitats (Matavelli et al. 2013; Iannuzzi et al. 2016; Nazaré-Silva and Silva 2021), can successfully thrive in this new habitat type in the Amazon.

When analyzing the entire dung beetle assemblages, diversity was lower in exotic pasture compared to native forest. Regarding the dung beetle diversity, habitat quality (e.g., temperature, humidity, soil properties), resource availability (quality and quantity) and evolutionary history of a region are determinants for species establishment (Hanski 1991; Scholtz et al. 2009). Since the Amazonian region of this study was originally covered and dominated by closed-canopy rainforest, we believe that originally there were few species that successfully inhabited open habitats. Subtropical and temperate ecosystems harbour a considerable diversity of dung beetles species that successfully uses open areas (Martínez-Falcón et al. 2018; Conover et al. 2019). For example, in mountain landscapes in Central Europe, open ecosystems (pasturelands) harbor a considerable higher diversity than native forested ecosystems (Tocco et al. 2013), which may have a marked importance for decision makers regarding the landscape future in this region. This is not only the case of Central Europe, but also for the temperate mountain (e.g., Escobar et al. 2007; Barragán et al. 2014; Moctezuma et al. 2016) and xeric plateau landscapes (e.g., Verdú et al. 2007) from North America. On the other hand, the scenario of the Amazon region is clearly distinct. Few species successfully occupy the niches available in pastures, resulting in a low diversity compared to forests. Nonetheless, while the number of species (0D) and abundant species (1D) were higher in forest than pasture, dominant species (2D) was similar between both habitats. Such a trend can be related to the assemblage dynamics established in both conserved and disturbed environments, in which a few species dominate the local assemblage (e.g., Halffter et al. 1992; Filgueiras et al. 2015; Correa et al. 2021a). In conclusion, although we observe an impoverished diversity in the Amazon pasture studied herein, it is important to consider that these landscapes were established recently (16 years). Dung beetle assemblages change throughout time (e.g., Escobar et al. 2008; Audino et al. 2014), and dung beetle species from conserved open ecosystems may invade recently established

pastures in tropical rainforest (Maldaner et al. 2021). Therefore, it is important to keep monitoring the novel agriculture-scenario that comes together with pasture expansion in the Amazon arc of deforestation.

Interestingly, habitat type affected each functional group differently, with paracoprid dung beetles being the most sensitive. Paracoprids feature the most diverse group among dung beetles (e.g., Escobar et al. 2008; Filgueiras et al. 2015; Correa et al. 2021a), with its species present different strategies and responses to environmental conditions. In a previous study conducted in Amazonian lowland forests, soil physical properties determined that paracoprid dung beetles are the most sensitive group due to their high diversity of strategies and behaviors (Salomão et al. 2022). Since tunnelling activity among dung beetles takes long time periods, which may take hours for tunnel building (Halffter and Edmonds 1982), we believe that long-term exposure to the harsh climatic conditions of open pasture strongly restrain paracoprid species. Following this rationale, telecoprid dung beetles usually present rapid food relocation behaviors (Latha and Thomas 2020), thus reducing the time length exposed to the environmental conditions compared to paracoprids. Considering the predominant closed-forest structure of tropical rainforests, the distinct environmental usage by paracoprid and telecoprid dung beetles may result in stronger environmental selection pressures of open habitats against paracoprid species.

The similar diversity patterns of endocoprid dung beetles between native forest and exotic pasture needs to be analyzed with care. Since we had a reduced number of species from this group ($S = 4$), we believe that the current statistical approach could have masked the differences in abundances observed between endocoprid groups collected in exotic pastures ($n = 5$) and native forest ($n = 241$), which were clearly distinct. In our opinion, the analysis of different functional groups with respect to the response of ecological assemblages to environmental conditions is fascinating but remains scarcely studied to date. Among dung beetle studies, there are a huge number of papers analyzing the effect of habitat type on their diversity in the tropics (e.g., Nichols et al. 2007; Filgueiras et al. 2015; Correa et al. 2020, 2021a). Thus, future meta-analysis studies could aid in proving whether there are general trends encompassing the role of habitat type on the different functional groups of dung beetles.

Agricultural expansion and the consequent conversion of tropical forests in pasturelands and other agriculture fields is inevitable. Nonetheless, by analyzing how such landscape transformation modifies biodiversity in different ecosystems, we can disentangle the resilience levels of native ecological communities to novel habitats such as pastures. In this study, pastures established in the Amazon region contained impoverished dung beetle assemblages when compared to the native forests. It is noteworthy that the conversion of tropical

rainforest ecosystem into non-native land-uses causes drastic negative impacts on biodiversity (Nichols et al. 2007; Santos-Filho et al. 2012; Pedrinho et al. 2018; Oliveira and Schmidt 2019). Nonetheless, while landscape transformations in many tropical rainforests comprise centuries of an intense process, Amazonian forests have been deforested intensely in recent decades. We believe that tropical ecological studies have achieved relatively advanced knowledge regarding long-term effects of deforestation on biodiversity (e.g., Bennett and Saunders 2010; Haddad et al. 2015), as well as landscape ecology (e.g., Arroyo-Rodríguez et al. 2020; Fahrig 2020). The relatively recent expansion of pasturelands in this portion of the Amazon is supported by our data. The absence of the widespread exotic paracoprid dung beetle *Digitonthophagus gazella* (Fabricius, 1787) (Pokhrel et al. 2020), reinforce the idea that this Amazonian region is facing a recent deforestation dynamic due to livestock. Having identified this trend early, we still have a chance to maintain Amazonian forest as the largest and most diverse tropical rainforest in the world, with public policies that allow unification of both the sustainable-use and the ecosystem conservation of the region.

Finally, because our sampling units were spatially autocorrelated (Moctezuma 2021), resulting in pseudoreplicates for each habitat type, we need to interpret the current results carefully, since we have a limited comprehension of the effects of habitat type on dung beetles' diversity in this region. Although our study is part of a scenario also recorded in other Amazonian landscapes, with abrupt losses in the diversity of dung beetles in exotic pastures compared to the native forest (e.g., Silva et al. 2017), a stronger sampling effort (i.e., sampling more spatially independent replicates) in future studies could reinforce and confirm the observed patterns.

Acknowledgements This paper is part of the Senior Project (Undergraduate in Agronomy) of MJGO and GCS. CMAC (Process 88887.603414/2021-00) and MAO (88887.717863/2022-00) thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) 'Bolsista CAPES/Brasil' for postdoctoral grant. RPS was supported by Dirección General de Asuntos del Personal Académico/UNAM. FZVM is a fellow of Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Brazil; 313397/2021-0).

Author contribution AP conceptualized and supervised the research project. MJGO and GCS collected the data. CMAC and FZVM performed the taxonomic identification of specimens. CMAC performed the statistical analyses. All authors participated in writing and manuscript review. All authors read and approved the final manuscript.

Declarations

Ethical approval This study was not invasive and complied with Brazilian law. At the end of the research, the dung beetle specimens were deposited in the "Entomological Section of the Zoological Collection at the UFMG (CEMT; Cuiabá, Mato Grosso, Brazil)" following standard procedures.

Conflicts of interest There are no any conflicts of interest about this research paper.

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