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From green to grey: Unravelling the role of urbanization on diversity of dung beetles in an Amazonian landscape

César M. A. Correa[1] · **Renato Portela Salomão**[3,4] · **Fredy Alvarado**[5] · **Elio Cesar Guzzo**[6,7] · **Kleyton Rezende Ferreira**[2,7]

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Abstract

The Brazilian Amazon has undergone an intense process of urbanization responsible for changes in the land use and land cover patterns in the last decades. Therefore, understanding the impacts resulting from the urbanization of Amazon become urgent, both to preserve biodiversity and associated ecosystem functions and services, since Amazon region comprise a key ecosystem regarding biodiversity and ecological dynamics. We studied, for the first time, the impact of urbanization on dung beetles, a recognized bioindicator group, in an Amazonian landscape. For this, we assessed the dung beetle taxonomic and functional responses along a preserved-rural-urban habitat gradient in an Amazonian city, and how landscape predictors affect dung beetle diversity. We found a consistent shift in species composition and reduction of both taxonomic and functional diversity from forest patches located outside the city towards those located in the city core. In addition, forest cover was the main driver of dung beetle responses at the landscape scale, where the increase of forest cover positively affected dung beetle diversity. Our results provide evidence that urbanization negatively impacts the dung beetle taxonomic and functional diversity in Amazonian cities, and reinforce the importance of maintaining forest cover to conserve dung beetles in tropical forests. Finally, the development of sustainable initiatives for the conservation of biodiversity in urban landscapes, such as public policies aimed at the maintenance of urban forest fragments, can help to maintain biodiversity and ecosystem processes within cities and to mitigate the urbanization impacts.

Keywords Amazon cities · Forest cover · Functional diversity · Taxonomic diversity · Tropical rainforest · Scarabaeinae

Introduction

Urban landscapes can change natural ecosystems and ecological communities in several ways, through alteration of land use and land cover, altering the biogeochemical cycles and modified biogeochemical cycles the biological conditions characteristics of urban environments (Hall et al. 2009). For example, the impervious surfaces caused by urban roads (physical transformation), the air and water contamination (chemical transformation), and the exotic species introduced in cities (biological transformation) are factors that come direct and indirectly with alterations of land cover promoted by urbanization, which promotes a challenging scenario for native biodiversity (McKinney 2008; Sanderson et al. 2018; Mella-Méndez et al. 2019). Such transformations in the natural and semi-natural ecosystems may lead to biological simplification, biotic homogenization, and even local extinction of native taxa (McKinney 2008; MacGregor-Fors and Escobar-Ibáñez 2017). Therefore, the maintenance of

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✉ César M. A. Correa
correa.agro7@gmail.com

[1] Laboratório de Bioecologia de Scarabaeoidea (Scaralab), Universidade Estadual de Mato Grosso do Sul, Aquidauana, Mato Grosso do Sul 79200-000, Brazil

[2] Instituto Federal de Educação, Ciência e Tecnologia de Mato Grosso, Juína, Mato Grosso 78320-000, Brazil

[3] Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Mexico

[4] Instituto de Ecología, Universidad Nacional Autónoma de México, Ciudad de Mexico, Mexico

[5] Instituto Potosino de Investigación Científica y Tecnológica (IPICYT), División de Ciencias Ambientales, San Luis Potosí CP 78216, SLP, Mexico

[6] Embrapa Tabuleiros Costeiros, Unidade de Execução de Pesquisa de Rio Largo, Rio Largo, Alagoas 57100-000, Brazil

[7] Universidade Federal de Alagoas, Programa de Pós-Graduação em Proteção de Plantas, Rio Largo, Alagoas 57100-000, Brazil

biodiversity in urban landscapes represents a challenge for biodiversity conservation (McKinney 2002, 2008). Maintaining healthy and diverse communities in urban landscapes is essential for human well-being, since ecological communities provision key ecosystem services (Bolund and Hunhammar 1999; Ziter 2016).

In the last decades, the Brazilian Amazon faced an important growth population, which increased from ca. 2.5 million in 1960 to ca. 28 million in 2015 (Tritsch and Le Tourneau 2016). Thus, this region has undergone an intense process of urbanization responsible for changes in the land use and land cover patterns (Tritsch and Le Tourneau 2016; Feng et al. 2017). Regarding the urbanization dynamics in Amazon, two aspects deserve special attention: (1) the urban expansion is much more recent when compared to other neighboring ecosystems, which results in (2) an ecosystem where most of the land cover is still conserved, with a reduced number of anthropogenic landscapes (Browder 2002; Vitel et al. 2009; Levis et al. 2017). Under such scenario, conserved ecosystems (e.g. Amazon forest) are more sensitive to anthropogenic landscape transformations compared to those that have been experiencing chronic intense transformations (Vitel et al. 2009; Levis et al. 2017). Studies in Amazon urban centers have already demonstrated that native animals (e.g. aquatic and terrestrial insects, birds, bats) and plants are negatively affected by urbanization (Monteiro-Júnior et al. 2015; Palheta et al. 2020; Rico-Silva et al. 2021; Soares et al. 2021). Nonetheless, such results apparently are context dependent, in which some groups of the ecological communities are negatively affected by the increased of urbanization, while others (e.g. exotic species) increase in more urbanized sites (Monteiro-Júnior et al. 2015; Martins et al. 2017; Rico-Silva et al. 2021). It is important to consider that public management strategies of greenspaces in Amazon cities are failing to establish appropriate practices that incorporate the spatial urban growth and their effects for the maintenance of biodiversity (Martins et al. 2017; Soares et al. 2021). Understanding the impacts resulting from the urbanization of Amazon becomes urgent, both to preserve biodiversity and associated ecosystem functions and services (Tritsch and Le Tourneau 2016; Ferreira et al. 2021).

The use of bioindicators is useful to understand the effect of spatial environmental variation, such as urbanization process, by providing rapid and relevant responses based on biodiversity (Goodsell et al. 2009; Gerlack et al. 2013). In this sense, dung beetles (Coleoptera: Scarabaeinae) are considered efficient indicators of environmental changes (Bicknell et al. 2014; França et al. 2016), present low cost for sampling (Gardner et al. 2008a), and are often used as focal organisms to assess urbanization impacts (Korasaki et al. 2013; Salomão et al. 2019; Correa et al. 2021a, b). They exhibit wide changes in their life history strategies that are reflected in easily measurable functional traits (Halffter and Edmonds 1982; Hanski and Cambefort 1991). Therefore, the dung beetles highlight as viable models for functional diversity studies (Barragán et al. 2011; Audino et al. 2014; Beiroz et al. 2018; Giménez Gómez et al. 2022). To our knowledge, there are no studies focusing on the effect of urbanization on dung beetle diversity in the Amazon region. Bioindicators may present distinct but complementary assessments of biodiversity responses to landscape transformation (Gardner et al. 2008b; Carvalho et al. 2020). Since Amazon region comprises a particular ecosystem regarding biodiversity and ecological dynamics, it is essential to understand how bioindicators respond to current challenges for biodiversity maintenance, such as the urban expansion.

Considering that there is a high demand but low supply of ecosystem services in urban landscapes (González-García et al. 2022), it is of uttermost importance to depict how urbanization drives biodiversity from different perspectives. However, the recognized importance of landscape structure changes to maintain biodiversity and related ecosystem functions remains very limited, especially when considering larger spatial scales in urban tropical landscapes (Walz and Syrbe 2013; Wu et al. 2013). Fortunately, with the advancement of geographic information and remote sensing tools (Steiniger and Hay 2009), many patterns are beginning to be revealed and described (Lechner et al. 2020). In this sense, the application of geographic spatial information has allowed us to understand important issues like the effect of changes in the intra-urban forest or the impact of grey *vs* green areas on urban biodiversity (Wellmann et al. 2020), as well as the effect of the heat island on species residing in urban environments (Mirzaei et al. 2020), highlighting the importance of including other urban variables under different landscape context. Therefore, a comprehensive analysis of the effects of urbanization on animal diversity requires taking other dimensions of diversity (e.g., taxonomic and functional) as well as landscape structure changes together (Kondratyeva et al. 2020).

In this study, we aimed to assess the effect of urbanization on dung beetle taxonomic (i.e. species richness) and functional diversity. More specifically, dung beetles were analyzed according to abundance, species richness, species composition, indicators species, functional richness, functional evenness, and functional dispersion. In order to analyze the effect of urbanization, we studied dung beetles along a preserved-rural-urban habitat gradient in an Amazonian city. In such gradient, we evaluated the effects of landscape structure (patch richness density, landscape heterogeneity and dominance) and composition (forest cover, edge density) on dung beetle assemblages. In addition, we assessed which of these landscape predictors were the most important drivers of dung beetle diversity.

It is important to consider that the anthropogenic matrices cause negative effects on biodiversity that inhabits the forest patches in its surroundings (Tabarelli et al. 2012; Filgueiras et al. 2015). Since the original and dominant land use of Amazon is closed-canopy forests, we expect that there is a decrease of abundance and diversity across the preserved-rural-urban gradient. In addition, the amount of natural habitat and the density of edge are two key parameters that drive diversity of dung beetles in the Neotropics, both in urban (e.g. Salomão et al. 2019) and in non-urban matrices (e.g. Souza et al. 2020; Estupiñan-Mojica et al. 2022). Thus, we expect that such landscape variables will be the most important drivers of beetle diversity in the urban landscapes of this study. Apparently, functional diversity presents a threshold regarding the land-use transformation scenario (Magioli et al. 2015; Rivera et al. 2021), in which the increase in the amount of native vegetation cover may not exhibit clear changes in functional diversity. We expect that response variables will be differently affected by urbanization process, with abundance and taxonomic diversity presenting more clear responses compared to functional diversity.

Methods

Study area

The study was carried out in the southern region of the Amazon Forest biome, in the Brazilian municipality of Juína, Mato Grosso, midwestern Brazil (11°26′55"S; 58°43′24" W; 320 m a.s.l.) (Fig. 1). The climate of the region, according to Köppen classification, is a transition between *Am* (tropical monsoon) and *Aw* (tropical hot-wet), with two well-defined seasons, the dry season from May to September and the rainy season from October to April (Alvares et al. 2014). The average temperature is 24 °C and the average annual precipitation is approximately 2,000 mm (Batistão et al. 2013). The native vegetation comprises tropical ombrophilous rainforest, which have been suffering from intense deforestation since the 80 s (see more of 'the arc of deforestation' in Gomez et al. 2015). Due to the urbanization dynamics in the region, there are forest remnants that are characterized by a mosaic of primary and secondary forests. The predominant vegetation physiognomy is the *terra firme* forest, although there are patches of floodable riparian vegetation (*varzea*).

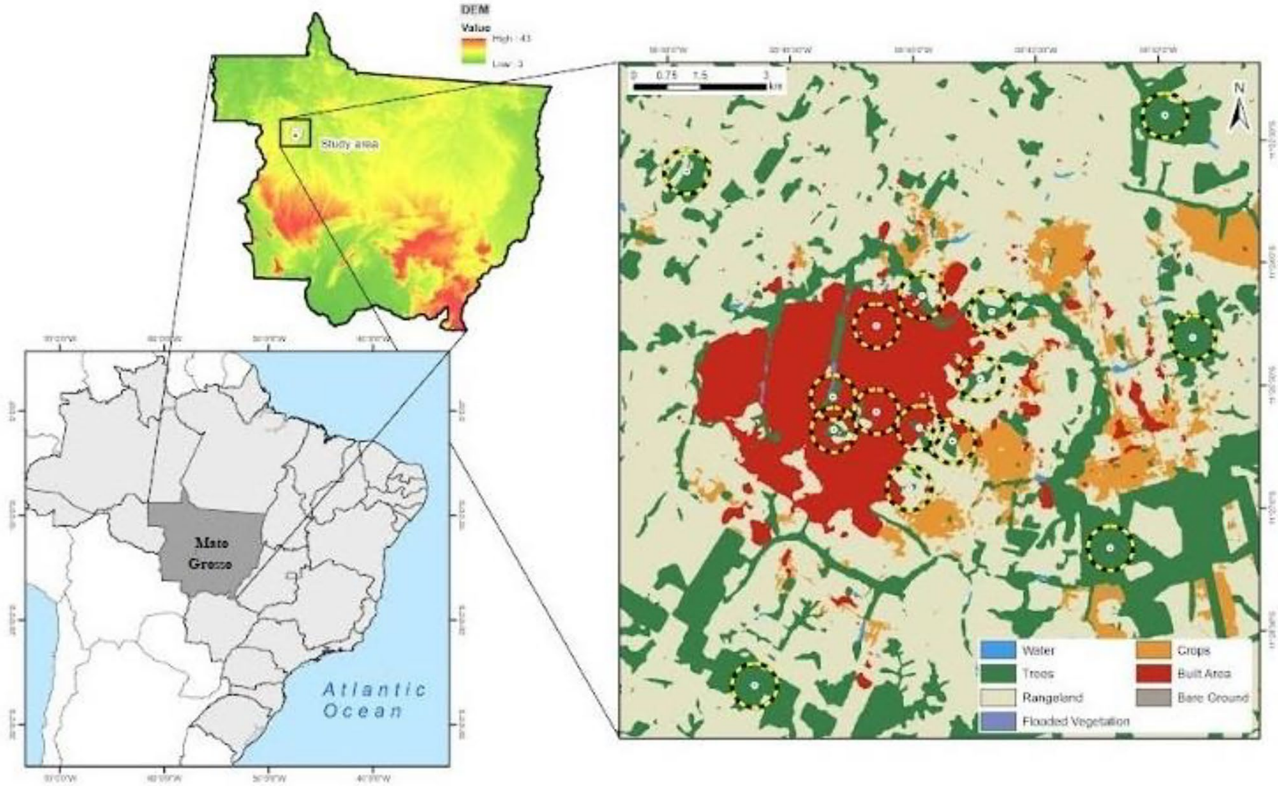

Fig. 1 Map of the study area located at Juína municipality, Mato Grosso, Brazil. The 15 studied sampling points are shown in circles located in the map, corresponding to the sites in which landscape composition and structure were obtained

Juína is one of the planned cities in an area of recent occupation in the State of Mato Grosso, Brazil (Gomes and Santos 2001), being founded in 1979. Currently, the municipality of Juína has a population of 41,190 and a population density of 1.50 inhabitants km^{-2}, of which approximately 87% live in urban areas, whereas 13% live in rural areas. The current population growth rate is 0.68%, which has been increasing since early 2000s (IBGE 2021).

Dung beetle sampling

We sampled dung beetles during the rainy season (April 2021), the most appropriate period to sample dung beetles in the region (Correa et al. 2021c). Beetles were collected in 15 sampling sites, each one consisting of forest fragment that was located near the core of Juína (hereafter 'urban fragment', n = 5 sites), in the borders of the city (hereafter 'rural fragment', n = 5), and outside of the city (hereafter 'preserved', n = 5 sites). Urban fragment sites are isolated from each other and surrounded by urban matrix which is composed of waterproof infrastructure characterized by residential buildings and unpaved roads with tree-lined streets. Rural fragment sites were surrounded by a mosaic of rural landscapes (e.g., plantation, livestock, rural fragments). Preserved forests are characterized by continuous and fragmented forests. In our study area, each sampling site was separated by at least 0.5 km from each other. The distance among sampling sites was used to ensure the independence among the samples (da Silva and Hernández 2015). In addition, we performed a Mantel test (Mantel 1967) 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 2022). We did not find spatial autocorrelation ($r = –0.11$; $P = 0.71$) ensuring a sampling independence in our study design.

At each sampling site, we placed a 300-m linear transect, 100 m away from its edge and delimited four sampling points along the transect (100 m apart from each other). At each sampling point, we set up two traps, 2 m apart, one baited with about 20 g of carrion (decaying beef) and the other with fresh human feces. We used different bait types to accurately represent the local dung beetle functional and trophic groups (Correa et al. 2016). In total, we had a sampling effort of 120 traps (2 traps * 4 sampling points * 15 sampling sites), 40 per habitat type (urban fragment, rural fragment, preserved).

Each trap consisted of a plastic container (15 cm diameter, 9 cm depth) installed at ground level, covered with plastic lids (15 cm diameter) supported with three wooden sticks (25 cm) to reduce desiccation of the bait and to avoid rainwater accumulation. Within each trap, 250 ml of a solution (salt + neutral detergent; 1.5%) was added. The baits were placed in plastic containers (50 ml) at the center of each trap using a wire as a bait holder. The traps remained active for 48 h at each site, after which the specimens were removed and packed in plastic bags containing 70% alcohol for further sorting and taxonomic identification.

Dung beetle traits

We analyzed three functional traits that are directly related to the ecosystem functions performed by dung beetles: body size, food relocation behaviour, and trophic preferences (see Giménez Gómez et al. 2022) (Table S1). We described the protocols used for trait assignments in the Supplementary Material.

Landscape descriptors

To measure the landscape structure in each of the 15 sampling sites, we estimated the area (in ha) of forest cover (land cover). Also, we estimated four land use categories (native forest, crops, cattle pastures, and human settlements) using a buffer of 500 m of radius centered on each fragment (Fig. 1). We obtained a supervised classification mapping using Sentinel-2 images from Global Visualization Viewer (GloVis) from April 2021 (10 m-spatial resolution) and using the ESRI ArcGIS 10.3 (Environmental Systems Research Institute) software, Spatial Analyst extension. We estimated landscape predictor variables using the land use and land cover classes on FRAGSTATS software version 4.0 (McGarigal et al. 2012). We estimated the following predictor variables: (i) percentage of forest cover (ha-^{1}); (ii) landscape heterogeneity [landscape diversity (Shannon index of land-cover types, SHDI)]; (iii) edge density [as the length of all forest edges per unit area (m/ha)], and (iv) NDVI (Normalized Difference Vegetation Index, which is a standardized way to measure healthy vegetation related with primary productivity).

The landscape variables used herein are commonly used to represent landscape structure changes (Fahrig et al. 2011), in addition to having been widely used in studies on the response of dung beetles at the landscape scales (Sánchez-de-Jesús et al. 2016; Alvarado et al. 2018a, b; Rivera et al. 2020). Forest cover is one of the most determinant landscape drivers of the spatial distribution of dung beetles and other biological groups in Neotropical forests (Enedino et al. 2018; Bonfim et al. 2021; Ratoni et al. 2023). Nonetheless, depending on the ecosystem studied, landscape heterogeneity may favor different portions of ecological communities, which have species that are benefited by the increase of the mosaic-pattern landscapes (Rivera et al. 2020; Estupiñan-Mojica et al. 2022). Also, forest cover per se may not always present a trustworthy approach of the amount of natural habitats in urban ecosystems, since many of these urban patches may encompass vegetations under different conservation status. Thus, NDVI would serve as a finer approach to assess the amount of conserved forests in the urban landscape of our study. Lastly, edge density comprises a key ecotone between different ecosystems and is determinant for dung beetle spatial dynamics (Souza et al. 2020; Salomão et al. 2023). The increase of its amount in the urban landscapes of our studies could be a proxy of a higher interaction between biotic and abiotic elements between forested and urbanized landscapes.

Data analysis

To assess the completeness of the survey for each of the habitat type, we estimated the sample completeness using the sample coverage analysis with 'iNext' package (see Chao et al. 2014; Hsieh et al. 2016). This is a measure of sample completeness and reveals the proportion of the number of individuals in an assemblage belonging to the taxonomic groups (i.e. species) represented in the sample. We estimated the sample coverages using an individual-based approach.

Dung beetle responses to habitat type

We used Generalized Linear Models (GLMs) to analyse the effects of habitat types (preserved, rural fragment and urban fragment) on dung beetle species richness and number of individuals. The assemblage attributes were the response variables, and habitat types were the explanatory variables. All GLMs were submitted to residual analysis to evaluate error distribution adequacy (Crawley 2013). Poisson errors corrected for overdispersion (quasi-Poisson) were used for dung beetle species richness and negative binomial errors for number of individuals. We undertook contrast analysis to test pairwise differences (Crawley 2013). Models with negative binomial errors were conducted with the package 'MASS' (Venables and Ripley 2002) were analysed in R software version 4.2.0 (R Core Team 2022).

To verify differences in assemblage structure among habitat types, we used Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson 2001). To test the heterogeneity of multivariate dispersions of samplings (i.e. sampling sites) among the different habitat types, we used Permutational Multivariate Analysis of Dispersion (PERMDISP) (Anderson 2001). The graphical exploration of the differences in assemblage structure of dung beetles among habitat types was performed by using Non-Metric Multidimensional Scaling (NMDS) (Anderson and Willis 2003). The NMDS ordinations, PERMANOVA and PERMDISP were performed based on the Bray-Curtis dissimilarity matrix, which is sensitive to species abundances. To reduce bias due to the discrepancies of species abundances, we transformed data (square-root). PERMANOVA, PERMDISP and NMDS were implemented in the Primer with PERMANOVA+ software version 6.0 (Clarke and Gorley 2006).

We used indicator value method following Dufrene and Legendre (1997), to identify dung beetle species that were significant and reliable indicators of each habitat type. We used 5,000 randomizations to determine the statistical significance of the observed indicator value (Monte Carlo test; $P < 0.05$). This analysis was performed with the 'indicspecies' package in R software (Cáceres et al. 2022; R Core Team 2022).

We calculated three functional diversity indexes that measure different aspects of functional diversity, a measure of diversity directly related to ecosystem functions (Cadotte et al. 2011; Hulot et al. 2020). Those indices were: 1) Functional dispersion (FDis) – represents the mean distance in multidimensional trait space of individual species to the centroid of all species (Laliberté and Legendre 2010); 2) Functional evenness (FEve) – measures the regularity of distribution and relative abundance of species in the functional trait space (Villéger et al. 2008); and 3) Functional richness (FRic) – represents the range of traits in a community quantified by the volume of functional trait space occupied (Villéger et al. 2008). Functional diversity indexes were calculated using the 'FD' package in R software (Laliberté et al. 2022; R Core Team 2022).

We used GLMs with a Gaussian distribution to assess the effects of habitat types in dung beetle functional diversity (FDis, FEve and FRic). All GLMs were submitted to residual analysis to evaluate error distribution adequacy (Crawley 2013) and conducted in R software (R Core Team 2022).

Dung beetle response to landscape descriptors

To analyze whether landscape structure (i.e., landscape heterogeneity, NDVI) and composition (i.e., forest cover, edge density) affected species richness, abundance and the above mentioned functional diversity indices, we fitted GLMs. For each model, appropriate distribution errors were used. The best models used explain the shifts of dependent variables were selected based on the Akaike Information Criteria (AIC). The significance of the dependent variables was tested using a likelihood ratio test between the full and the reduced model using the lmtest package (Zuur et al. 2009; Hothorn et al. 2022). The variables that were excluded in the most parsimonious models were considered non-significant. Normality of the residuals was visually assessed from normal q–q plots, and the presence of outliers was tested using Cook's distance. All analyses were performed using R software (R Core Team 2022).

To assess the most important drivers of dung beetle assemblage at landscape scale, we used a hierarchical partition analysis (Chevan and Sutherland 1991). We compared the relative and independent importance of our four explanatory variables for species richness, abundance, and functional diversity. Hierarchical partitioning is a multiple-regression technique in which all possible linear models are considered together to establish the most probable predictors while minimizing the influence of multicollinearity and providing an independent contribution from each explanatory variable (see Costa et al. 2022). Models were assessed based on the R^2 adjustment, which allowed us to interpret the independence of effects as a proportion of the variance explained by the total model. For each model, appropriate distribution errors were used. The significance of independent effects for each explanatory variable was calculated by randomized tests with 1,000 permutations (Mac Nally 2002; Olea et al. 2010) using the 'hier.part' package in R software (Walsh and Nally 2013; R Core Team 2022).

Results

Dung beetle response to habitat type

We collected a total of 4,298 dung beetle individuals belonging to 17 genera and 66 species. A total of 58 species (N = 2,521) was recorded in preserved sites, 48 species (N = 1,081) in rural fragments and 25 species (N = 696) in urban fragments (see Table S2). The sample coverage estimator revealed a high sampling efficiency (> 98% in all habitat types) (Table S2). This indicates that we had an adequate effort to represent the dung beetle assemblages in our sampling sites.

Species richness per sampling site ranged between 26 and 41 in preserved forests, between 7 and 32 in rural fragments, and between 8 and 15 in urban fragments (Table S2). The species richness was higher in the preserved forests, followed by rural fragments, being urban fragments the least speciose habitat ($F_{2,12} = 14.16$, $p < 0.01$ – Fig. 2A). Regarding dung beetle abundance, preserved forests had between 249 and 671 individuals recorded in each sampling site, rural fragments ranged from 52 to 323 individuals, while urban fragments recorded between 62 and 340 individuals (Table S2). The number of individuals was higher in the preserved forests than in rural and urban fragments, which did not differ in their abundances ($\chi^2_{2,12} = 10.08$, $p < 0.01$ – Fig. 2B).

Nineteen species were recorded in all three habitat types (Fig. S1). The preserved forests had 15 species recorded exclusively in this habitat and shared 22 species with rural fragments and two species with urban fragments (Fig. S1). Four species were recorded exclusively in rural fragments, and this habitat shared three species with urban fragments (Fig. S1). Only one species (*Canthon conformis*) was exclusively collected in urban fragments (Fig. S1).

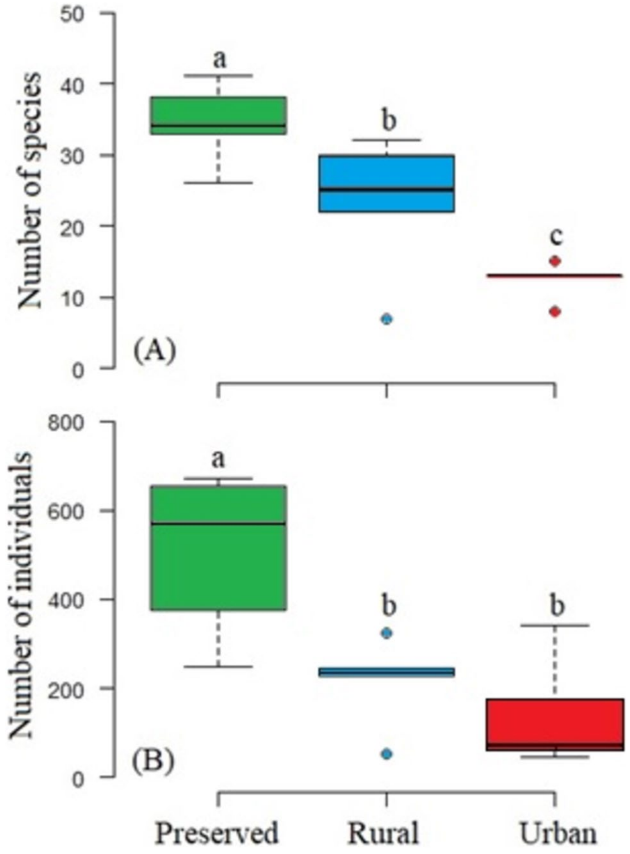

Fig. 2 Average species richness (**A**) and abundance (**B**) of dung beetles sampled in preserved, rural and urban forests in an Amazonian landscape, in Juína, Mato Grosso, Brazil. Different letters above the bars indicate statistically significant differences ($P < 0.05$). Error bars represent ± SE

NMDS ordination showed distinct groups, corresponding to the three habitat types, where all of them were significantly different from each other (Pseudo-F = 4.29; $P < 0.01$ – Fig. 3, Table S3). The different habitats did not show differences in the multivariate dispersion of points (Permdisp-F = 1.13; $p = 0.64$ – Fig. 3, Table S3). Finally, of the 66 species analyzed, 11 species were considered indicators of preserved forests, two indicator species of urban fragments (*Canthidium* sp. 4 and *Canthon histrio*), but no species were indicators of rural fragments (Table 1).

FDis ($F_{2,12} = 0.04$; $p = 0.95$ – Fig. 4A) and FEve ($F_{2,12} = 2.62$; $p = 0.11$ – Fig. 4B) did not significantly differ among habitat types. On the other hand, FRic was higher in the preserved forests, and similar in the rural and urban fragments ($F_{2,12} = 9.74$; $p < 0.01$ – Fig. 4C).

Dung beetle response to landscape descriptors

Among the landscape descriptors, Shannon diversity and NDVI did not affect dung beetle diversities and abundance.

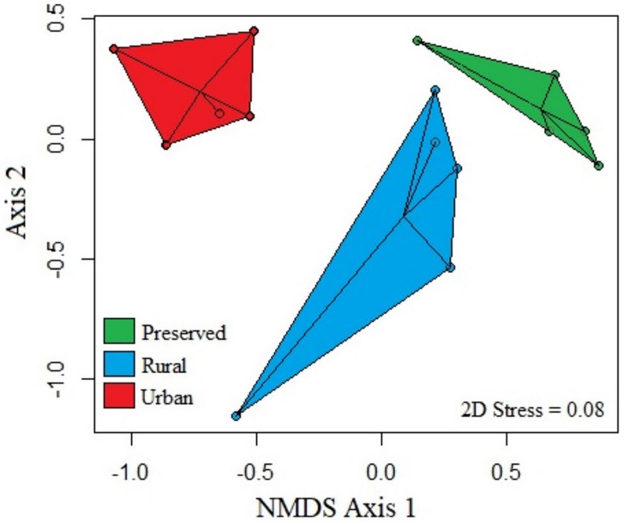

Fig. 3 Distribution patterns (NMDS) of the sampling points comparing assemblage structure (Bray-Curtis similarity) of dung beetles among preserved, rural and urban forests, and dispersion of points to centroid (lines), in the urban Amazonian landscape of Juína, Mato Grosso, Brazil

Nonetheless, forest cover and edge density were the landscape descriptors that best explained shifts in beetle diversity (Table 2). The increase of forest cover positively affected dung beetle species richness, abundance, and FRic (Fig. 5). Nonetheless, the increase of edge amount had a negative effect on species richness.

Hierarchical partitioning and randomization tests reinforced our model comparisons by revealing the independent and significant influence of our landscape predictors on dung beetle taxonomic and functional diversity. Forest cover had the highest individual contribution to dung beetle species richness, abundance, FEve and FRic, making up 62.5%, 67.2%, 69.5% and 58.2% of the explained variance in hierarchical partitioning, respectively (Fig. 6A–D).

Table 1 Indicator value (IndVal) of dung beetle species sampled in preserved, rural and urban forest fragments in an Amazonian landscape

Taxon	IndVal	*P* value	Habitat
Ateuchus aff. *murrayi*	0.800	0.010	Preserved
Ateuchus sp. 1	0.666	0.015	Preserved
Canthidium sp. 4	0.686	0.026	Urban
Canthidium sp. 12	0.800	0.014	Preserved
Canthon histrio	0.787	0.016	Urban
Canthon fulgidus	0.970	0.004	Preserved
Dichotomius aff. *lucasi*	0.928	0.002	Preserved
Dichotomius mamilatus	0.846	0.007	Preserved
Dichotomius melzeri	0.666	0.018	Preserved
Eurysternus atrosericus	0.693	0.019	Preserved
Onthophagus onorei	0.761	0.023	Preserved
Onthophagus rubrescens	0.702	0.035	Preserved
Scybalocanthon sp. 1	0.676	0.023	Preserved

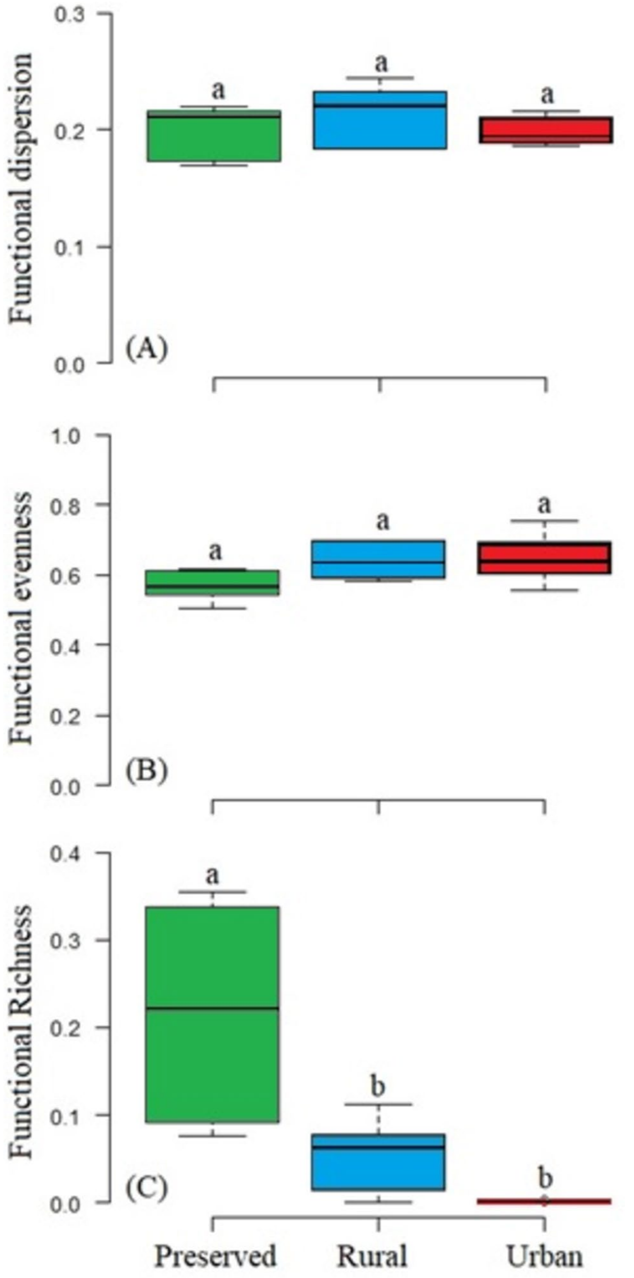

Fig. 4 Average functional dispersion (**A**), functional evenness (**B**) and functional richness (**C**) of dung beetles sampled in preserved, rural and urban forests in Juína, Mato Grosso, Brazil. Different letters above the bars indicate statistically significant differences ($P < 0.05$). Error bars represent ± SE

Table 2 Statistical models analyzing the effect of landscape variables on taxonomic and functional diversity of dung beetles. Models shown in bold indicate statistically significant effect

	Forest cover	Edge amount	Shannon diversity	NDVI
Taxonomic diversity				
Species richness	**$X^2_{1,12}=24.94$; $P<0.01$ (+)**	**$X^2_{1,12}=6.34$; $P=0.01$ (-)**	NS	NS
Abundance	**$X^2_{1,12}=13.96$; $P<0.01$ (+)**	$X^2_{1,13}=3.36$; $P=0.06$	NS	NS
Functional diversity				
Functional dispersion	$F_{1,13}=0.11$; $P=0.74$	NS	NS	NS
Functional evenness	$F_{1,13}=3.40$; $P=0.08$	NS	NS	NS
Functional richness	**$F_{1,13}=11.58$; $P<0.01$ (+)**	NS	NS	NS

Models shown in bold indicate statistically significant effect

NS variables not selected by the best models, "(+)" positive relationship, "(-)" negative relationship

Discussion

Dung beetle taxonomic and functional response along a preserved-rural-urban gradient in the Brazilian Amazon

The species richness and abundance of dung beetles were higher in preserved sites than in rural and urban fragments. These results corroborate the findings of Korasaki et al. (2013) and Salomão et al. (2019) in Atlantic Forest, and Correa et al. (2021a, b) in the Brazilian Cerrado, who also found that urbanization negatively affected dung beetle species richness and abundance. Overall, dung beetle assemblages from tropical forests are greatly influenced by three factors: *i*) vegetation structure (Halffter and Arellano 2002; Gardner et al. 2008a; Costa et al. 2017); *ii*) availability of mammalian dung resources (Nichols et al. 2009; Bogoni et al. 2019; Raine and Slade 2019) and *iii*) microhabitat conditions (Larsen 2012; Davis et al. 2013). The low species richness and abundance in forest patches located in the core of urban areas indicate that, although such remnants maintain ecological communities, they are

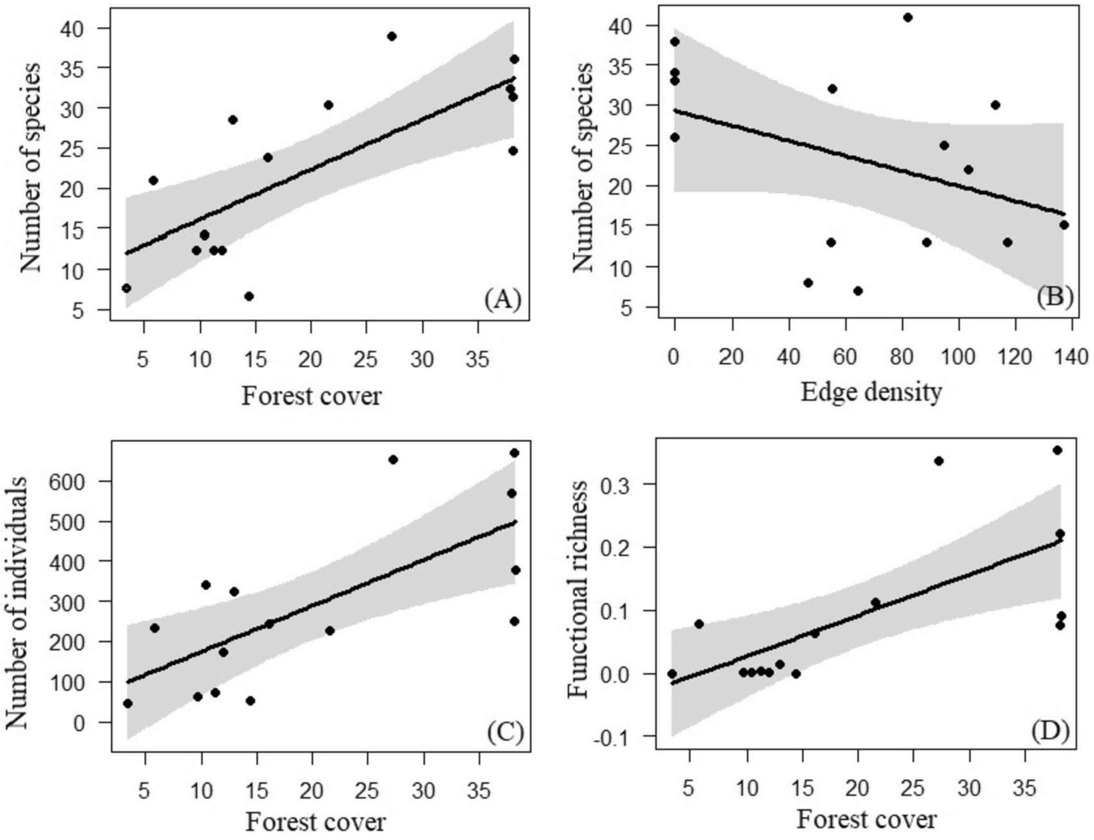

Fig. 5 Best-fit models showing the responses of dung beetle species richness (**A**, **B**), abundance (**C**), and functional richness (**D**) to forest cover and edge density. Black dots represent the 15 plots where dung beetles were surveyed in Juína, Mato Grosso, Brazil. Grey shadows show represent the 95% confidence intervals of the models

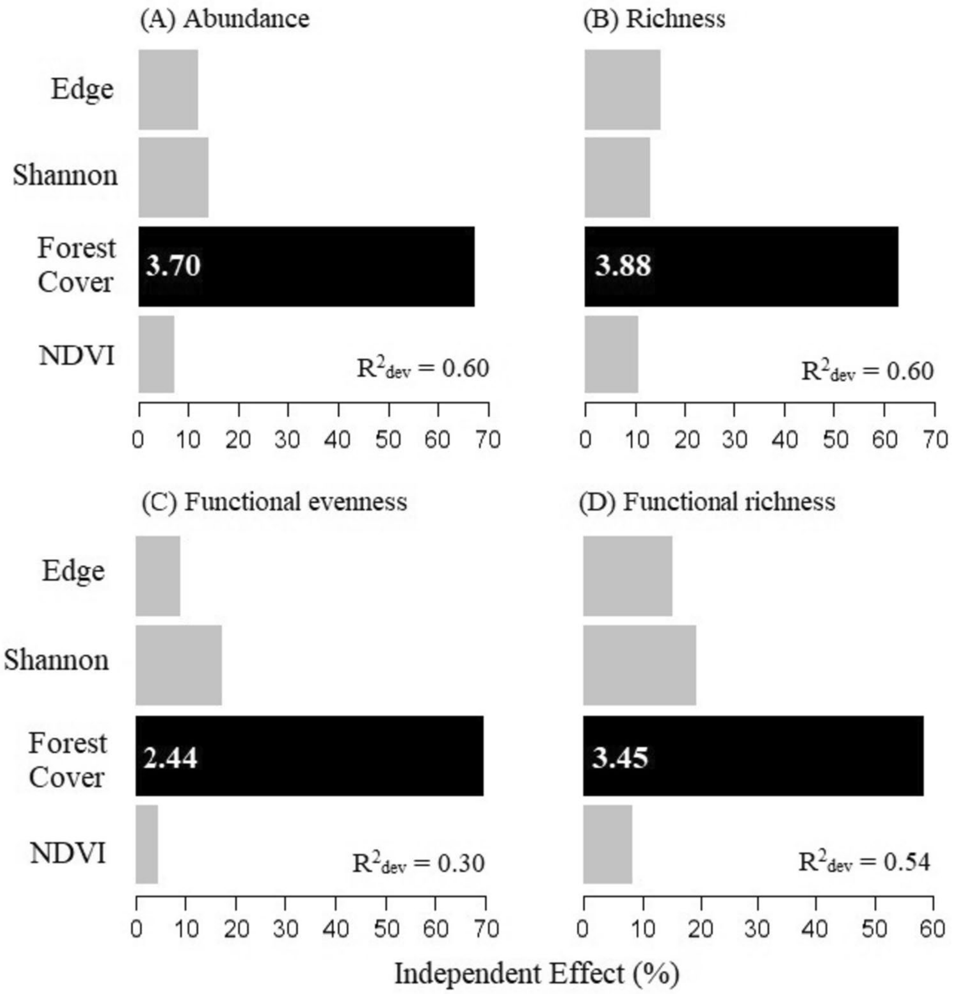

Fig. 6 Distribution of percentage of independent effects of different predictors of dung beetle taxonomic and functional diversity in Juína, Mato Grosso, Brazil. The x-axis represents the percentage of independent effects (IE%). Black bars represent significant effects ($\alpha = 0.05$) established by randomized tests. R^2_{dev} is the total variation of data explained by the model. Z values for distributions obtained through 1,000 randomizations were calculated as indicators of the significance based on the 0.95 ($Z \geq 1.65$) confidence interval

highly impoverished when compared to the patches located in the city surroundings. It is important to consider that forest fragments located outside the city of Juína (preserved forests) are larger than rural fragments. The observed effects of habitat type on urban fragments in this study are in accordance with previous fragmentation studies (Nichols et al. 2007; Filgueiras et al. 2015), in which smaller fragments (which were our urban fragments) retain a lower diversity compared to larger ones (rural fragments and preserved ones). Cities highlight as an important element of the landscape matrix that can present novel scenarios and trends regarding the paradigm of habitat loss and fragmentation (Fahrig et al. 2022). As Amazon region comprises a relative pristine tropical ecosystem when compared to other Neotropical ecosystems (e.g. Cerrado, Atlantic Forest), biodiversity resilience to urbanization and to forest fragmentation are potentially distinct. In order to disentangle the effects of forest fragmentation from urbanization ones, future studies should aim at analyzing patches of different sizes throughout the spatial gradient that comprises the urban core and surroundings.

We found that dung beetle assemblage structure differed among preserved sites, rural and urban fragments. The fragmentation of natural habitats, caused by urbanization, modifies microclimatic factors (abiotic and/or biotic factors), including soil temperature, air pollution and insect trapping by artificial light (McKinney 2008; Chen et al. 2010; Edmondson et al. 2016). In addition, physical changes along the gradient preserved-rural-urban strongly influence available habitats for native species (McKinney 2008). Therefore, the new abiotic conditions imposed on dung beetles by urbanization can directly affect the biology, dispersion, and colonization ability of species (Hanski and Cambefort 1991), modifying the assemblage structure of the dung beetles (Correa et al. 2021a). Thus, animal species that successfully occupy forest fragments in urban landscapes survive under climatic conditions highly contrasting from those observed in conserved forests or in rural landscapes (McKinney 2008; Huang et al. 2009; Grimm et al. 2011). However, the presence of well-defined assemblages in each habitat type highlights the importance of each of them for conserving diversity of dung beetles in the landscape studied. Indeed, urban fragments can provide refuges for dung beetles in the urban matrix (see Korasaki et al. 2013; Salomão et al. 2019; Correa et al. 2021a), while rural fragments may help to maintain biodiversity and their associated ecological functions in agricultural landscapes (Gray et al. 2014). Our results may indicate that, although dung beetle assemblages from Amazon region are highly sensitive to urbanization, there are groups of species that are maintained even in the most urbanized remnants of a city.

Even though we detected changes in dung beetle richness and assemblage structure along preserved-rural-urban gradient, the presence of indicator species in preserved forests and urban fragments suggest that dung beetle species respond differently to urbanization effects (see Salomão et al. 2019; Correa et al. 2021a). In the case of indicator species of preserved forests, they are more susceptible to changes in habitat (McGeoch et al. 2002), and in many cases may be restricted to certain habitat types or conditions (*e.g.*, forest-dependent species; see da Silva et al. 2019). Among indicator species of preserved forests, *Canthon fulgidus* is commonly found in primary and secondary Amazonian forests, perching on larger leaves exposed to sunlight in the forest understory from 0.50 to 2.5 m high (Nunes et al. 2018; Ferreira et al. 2020). *Dichotomius mamillatus*, *Dichotomius melzeri*, *Eurysternus atrosericus*, and *Onthophagus rubrescens* have a wide distribution in the Amazon and are recorded in forest fragments with different degrees of conservation in the Brazilian Amazon (Silva et al. 2016, 2022; Cajaiba et al. 2017; Ferreira et al. 2020). Thus, with the increase in the urbanization these species are the most susceptible for extinction in urban landscapes in the Amazon Forest. In contrast, urban fragments can offer advantages to opportunistic species and species more tolerant to the changes in the environmental dynamics (e.g. matrix-tolerant species; see da Silva et al. 2019), that result in an increase of their populations. In our study, *Canthon histrio* was considered indicator of urban forest. It is a habitat generalist species widely distributed in Brazilian landscapes that is commonly found in native forest fragments of varying sizes and degrees of conservation (Silva et al. 2016; Ferreira et al. 2020), as well as in open environments such as Amazonian pastures (Silva et al. 2016; Cajaiba et al. 2017; Puker et al. 2024). It is important to consider that most species were classified as indicators of preserved site. We believe that this reflects the history of the region, which was originally covered by forested sites, thus comprising the environmental scenario in which species adapted to inhabit in Amazon. Since urbanized fragments are structurally less conserved (Salomão et al. 2019), the few indicators of urban fragments in the current study could be related to the expansion of species that benefit from open-habitat conditions that come from the expansion of the arc of deforestation in Amazon region (França et al. 2021; Maldaner et al. 2021).

Until now, there has been very little information on the effects of urbanization on dung beetle functional diversity in Neotropical region (see Correa et al. 2021a, b). We found that functional richness (FRic) was higher in the preserved forests, while functional dispersion (FDis) and functional evenness (FEve) did not differ among habitat types. This lack of difference of FDis and FEve among the habitat types can be an indication that only the identity of traits (FRic) is being influenced by urbanization and not the structure of the functional assemblage. Similar FDis values may indicate a higher dispersion of functional traits in rural and urban fragments corresponding to a gain in the variability of responses to urbanization disturbances among species that contribute in a similar way to the ecosystem function (Laliberté and Legendre 2010). Similar FEve values suggest that the space of the functional niche is being uniformly occupied by dung beetle species (see Audino et al. 2014; Correa et al. 2021a). Thus, Amazonian dung beetles may show characteristics that allow them to tolerate the environmental conditions created by the urbanization disturbance, where the niche space occupied in rural and urban fragments is really being exploited (Barragán et al. 2011; Audino et al. 2014; Correa et al. 2019, 2021a). An alternative hypothesis is that our results are context dependent. Since Juína is a relatively small city in Amazon region compared to Manaus – ca. 2,250,000 inhabitants, and Belém – ca. 1,500,000 inhabitatns (IBGE 2021), it is possible that in Amazon metropolitan regions the effects of urbanization on functional diversity may differ. Finally, the lower FRic values found in rural and urban fragments suggest a loss of functionally specialized species in these areas, causing low stability through time and reduction in ecosystem processes provided by dung beetles (Cadotte et al. 2011; Díaz and Cabido 2011; Audino et al. 2014). The decrease of ecosystem services such as nutrient cycling, seed dispersal (Nichols et al. 2008) and reduction of fecal helminth transmission that cause human diseases (Nichols and Goméz 2014) in urban ecosystems can indirectly affect human life quality in the urban landscapes (see Correa et al. 2021a).

Landscape descriptors as drivers of dung beetle responses in a preserved-rural-urban gradient

Our results demonstrated that forest cover was the main driver of changes in dung beetle diversities, and the decrease in forest cover led to low dung beetle species richness, abundance, FEve and FRic. The loss of forest cover is associated with the reduction of diversity and abundance of mammals, the main resource providers for the dung beetles (Raine and Slade 2019), in urban areas (McKinney 2008; Villaseñor et al. 2014), which directly impacts the presence of excrement, which is a key factor for the maintenance of populations of dung species. Besides, the increase in forest edges restrained dung beetle species richness. In the tropics, the loss of native green areas due to urbanization apparently follows the same trend observed in other human-made matrices, as pasturelands (Alvarado et al. 2018b), plantations (Beiroz et al. 2019), and water cover due to hydroelectric (Storck-Tonon et al. 2020). In our opinion, the message in clear: the loss of tropical forests comes with a linear decrease of biodiversity, which is simplified both taxonomically and functionally. Nonetheless, we need to be careful, because there are clear differences among the ecosystems regarding the negative effects of the loss of forest cover and increase in the amount of edge. For example, in the fragmented landscape of the Atlantic rainforest, located in South America, the amount of edge apparently is the most important driver of biodiversity changes, negatively affecting dung beetle assemblages (Souza et al. 2020). Notwithstanding, in the Northernmost tropical rainforest of Americas, in Mexico, landscape heterogeneity is the most important driver of changes in dung beetle assemblages (Alvarado et al. 2018b; Rivera et al. 2020). In our study, landscape heterogeneity (i.e. Shannon Diversity of land use) did not affect beetle diversity, being landscape composition the most important drivers. Since Amazon region is suffering from a relative recent intense landscape transformation (but see Levis et al. 2017), its communities are still pristine when compared to other tropical ecosystems. Pristine ecosystems are much more sensitive to landscape changes than chronically disturbed ones (Melo et al. 2013). This marked sensitiveness may explain the clear effect of forest cover, a much more direct landscape predictor, instead of other landscape variables.

Precisely, our results highlight the importance of the amount of native forest habitat in Amazonian cities (Rico-Silva et al. 2021; Fragata et al. 2022). According to the habitat amount hypothesis the species richness in a habitat site increases with the amount of habitat in the 'local landscape' defined by an appropriate distance around the site, with no distinct effects of the size of the habitat patch in which the site is located. This, in practice and based on our results, suggest that, in order to optimize biodiversity conservation in urban Amazonian landscapes, land-sparing models may be appropriate (Ibáñez-Álamo et al. 2020). It has been argued that buildings interspersed with green patches that concentrate biodiversity-supporting vegetation are the best approach for cities. Thus, the development of sustainable initiatives for the conservation of biodiversity in urban landscapes, such as public policies aimed at the maintenance of urban forest fragments, can help to maintain biodiversity within cities (MacGregor-Fors et al. 2016). Finally, our results are part of a scenario also recorded in other tropical landscapes (e.g., Korasaki et al. 2013; Salomão et al. 2019; Correa et al. 2021a, b, c), demonstrating a negative impact of urbanization on dung beetle assemblages. However, it is essential to highlight that, given the spatial limitations of our study (e.g., a single city location), and due to the large heterogeneity and size of the Amazon, additional research across the Amazon region is essential to gain a more nuanced insight into dung beetle responses to urbanization in this tropical ecosystem.

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Authors' contributions CMAC and RPS wrote the manuscript and analyzed the data, FA wrote the manuscript and obtained the landscape variables. ECG and KRF performed the experiments and reviewed the manuscript. All authors reviewed the manuscript.

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Declarations

Ethical approval The experimentation was no invasive and complied with Brazilian law.

Competing interests The authors declare no competing interests.

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