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PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA – PPG-ECO

COMO A ESTRUTURA DA PAISAGEM AFETA AS ASSEMBLEIAS DE ROLA-BOSTAS EM CIDADES AMAZÔNICAS?

VANESSA PONTES MESQUITA

Manaus, Amazonas

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Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requerimentos para obtenção do título de mestre em Biologia (Ecologia).

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ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 17 dias do mês de Novembro do ano de 2022, às 09h00min, por videoconferência, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: a Dra. **Diana Abilene Ahuatzin Flores**, El Colegio de la Frontera Sur – ECOSUR, o Dr. **Fabio Correia Costa**, da Universidade Federal de Pernambuco – UFPE e o Dr. **João Carlos Pena**, da Universidade Federal de Goiás – UFG, tendo como suplentes o Dr. Marcelo Gordo, da Universidade Federal do Amazonas – UFAM e a Dra. Priscila Paixão Lopes, da Universidade Estadual de Feira de Santana – UEFS, sob a presidência do orientador, a fim de proceder a arguição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **VANESSA PONTES MESQUITA**, intitulado: **"COMO A ESTRUTURA DA PAISAGEM AFETA ASSEMBLEIAS DE BESOUROS ROLA-BOSTA EM CIDADES AMAZÔNICAS?"**, orientada pelo Dr. Renato Portela Salomão, do Instituto Nacional de Pesquisas da Amazônia – INPA e co-orientada pela Dra. Cintia Cornelius Frische, da Universidade Federal do Amazonas – UFAM.

Após a exposição, o discente foi arguido oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

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Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

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Sinopse:

Estudou-se como a estrutura da paisagem em áreas urbanas impacta a diversidade de besouros escarabeídeos em munícipios do estado do Amazonas, Brasil. Aspectos como abundância, riqueza, tamanho corporal e grupos funcionais de dieta e nidificação foram avaliados.

Palavras-chave: Amazônia, Coleoptera, Fragmentação, Habitat, Urbanização

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“Passava os dias ali, quieto, no meio das coisas miúdas. E me encantei.”

Manoel de Barros

RESUMO

No mundo, o crescimento das cidades é um dos principais responsáveis diretos e indiretos pela perda de cobertura vegetal nativa. Na Amazônia, as transformações de paisagem relacionadas a urbanização vêm causando a substituição das áreas naturais por paisagens urbanas. Estas alterações afetam diretamente as comunidades biológicas que residem em remanescentes florestais inseridos nas cidades, comprometendo a manutenção dos ecossistemas urbanos e naturais. Neste trabalho buscou-se entender como as modificações na paisagem afetam assembleias e grupos funcionais (i.e. dieta e estratégia de remoção de recurso) e tamanho corporal como atributo funcional de besouros rola-bosta em cidades da Amazônia Central. Foram analisados 38 fragmentos florestais urbanos em seis municípios pertencentes a região metropolitana de Manaus, Amazonas. Se analisou a relação da cobertura florestal, área agrícola, densidade de borda e número de fragmentos na paisagem, sobre a diversidade de rola-bostas. A perda de cobertura florestal foi o fator mais determinante, afetando negativamente a riqueza de espécies, abundância e tamanho corporal, tanto total como nos diferentes grupos funcionais. A maior densidade de borda afetou positivamente o grupo funcional de rola-bostas cavadores. O maior número de fragmentos próximo aos fragmentos amostrados afetou negativamente a abundância de generalistas de dieta, riqueza de residentes e tamanho de coprófagos. Tais resultados demonstram que as mudanças na diversidade ecológica causadas pela urbanização são impulsionadas por diferentes parâmetros da paisagem, e cada um está exercendo pressão sobre diferentes aspectos das assembleias. Este estudo contribui para a compreensão de como a mudança na quantidade e distribuição da cobertura florestal em cidades tropicais afeta diferentes grupos funcionais de rola-bostas que residem em fragmentos florestais.

ABSTRACT

In the world, the growth of cities is one of the main direct and indirect factors responsible for the loss of native vegetation cover. In the Amazon, landscape transformations related to urbanization have been causing the replacement of natural areas by urban landscapes. These changes directly affect the biological communities that reside in forest remnants inserted in cities, compromising the maintenance of urban and natural ecosystems. This work sought to understand how changes in the landscape affect assemblages and functional groups (i.e. diet and resource removal strategy) of dung beetles in cities in Central Amazonia. 38 urban forest fragments were analyzed in six municipalities belonging to the metropolitan region of Manaus, Amazonas. Among the landscape variables analysed (i.e. forest cover, agricultural area, edge density and number of patches around the fragment) forest cover was the most determining factor, negatively affecting species richness, abundance and general body size, and also the different functional groups (i.e. diet and resource removal strategy). Higher edge density positively affected the tunneller functional group. The largest number of fragments negatively affected the abundance of diet generalists, dweller richness and coprophagous body size. These results demonstrate that changes in ecological diversity caused by urbanization are driven by different landscape parameters, and each is exerting pressure on different aspects of assemblages. This study contributes to the understanding of how changes in the amount and distribution of forest cover in tropical cities affects the taxonomic diversity of dung beetles assemblages.

SUMÁRIO

INTRODUÇÃO GERAL

A urbanização é um processo antropogênico que envolve o crescimento e adensamento populacional em cidades, resultando em processos de extensão territorial dos centros urbanos (Moll et al, 2019). A crescente concentração humana nas cidades demanda aumentos na disponibilidade de energia, espaços e recursos naturais (Marzluff et al, 2001; Elmqvist et al, 2013). Por meio de diferentes usos da terra, as atividades humanas alteram os processos e a estabilidade dos ecossistemas naturais (Deng et al, 2021). Concomitantemente com o crescimento das áreas urbanas, há um processo de fragmentação e perda de ambientes naturais. A paisagem urbana, composta por remanescentes florestais com diferentes distribuições espaciais, circundados por uma matriz composta majoritariamente por superfícies impermeáveis (i.e. superfície não natural de solo compactado, asfaltado, com concreto) (Parris, 2016; Magura et al, 2020), desafiando a manutenção das comunidades de áreas florestadas. Além disso, distúrbios ambientais causados pelo aumento da urbanização podem resultar em perda ou redução de habitat adequado para comunidades nativas, introdução de espécies exóticas e mudanças na qualidade do habitat e disponibilidade de alimentos (McKinney, 2002; Kowarik, 2011).Neste sentido, o ambiente urbano gera mudanças na estrutura de comunidades ecológicas nativas, levando à diminuição da diversidade e abundância e de espécies (Violle et al, 2007; McKinney, 2008; Aronson et al, 2014).

Na Amazônia brasileira, as áreas urbanas evoluíram com o surgimento de cidades de porte intermediário e a multiplicação de pequenos centros urbanos, que seguem as rotas das principais rodovias e rios da região (Sathler et al, 2009). Apesar de ser uma região que historicamente vem sendo alterada por atividades antrópicas (Macedo at al., 2021), a Amazônia ainda apresenta uma grande porção de cobertura florestal nativa. Neste sentido as regiões não urbanizadas da Amazônia apresentam uma condição relativamente pristina (i.e. mata preservada, intocada) principalmente quando comparada a outras florestais tropicais (Vitel et al, 2009, Levis et al, 2017). Além do incipiente conhecimento relativo aos efeitos da urbanização sobre a diversidade ecológica na Amazônia (Morris et al, 2010), a matriz florestal que circunda as cidades deste ecossistema representa um cenário singular referente as dinâmicas de urbanização nos trópicos. Através do conhecimento sobre os efeitos da urbanização em cidades da Amazônia, é possível aprofundar a compreensão sobre a resiliência das comunidades ecológicas frente a transformações abruptas nas paisagens tropicais.

Entre as diversas ferramentas para compreender os efeitos de alterações na paisagem, a ecologia da paisagem se destaca como uma ferramenta que ajuda a entender como os diferentes padrões de organização espacial das unidades da paisagem influenciam seu funcionamento (Metzger, 2001). Os ambientes urbanos se mostram como modelos bastante apropriados para a compreensão dos efeitos da estrutura e composição da paisagem sobre a biodiversidade. As diferentes quantidades e disposições de remanescentes florestais urbanos podem ser fatores determinantes para a vulnerabilidade dessas áreas. Aspectos locais como a estrutura e a complexidade da vegetação afetam a qualidade desses remanescentes, atuando como filtros ambientais influenciando diretamente a restrição ou permanência de espécies capazes de ocupar esses espaços (Gallé et al, 2022). Mudanças na cobertura do solo e na configuração da paisagem levam à homogeneização biótica em áreas perturbadas (Gámez-Virués et al, 2015). Esta consiste no aumento da similaridade taxonômica, funcional e genética de duas ou mais comunidades no espaço e no tempo, e é reconhecida como o processo de simplificação biológica do ecossistema (Dornelas et al, 2014; Bittencourt et al, 2019). Como consequência direta, há uma redução na prestação de serviços ecológicos (p.e. produção de alimentos e matérias-primas, regulação do clima, conservação do solo e biodiversidade) (McDonald et al, 2013). Estes serviços são prestados pelas comunidades nativas, sendo essenciais para a manutenção dos ecossistemas urbanos e não urbanos (Tolessa et al, 2017; Liu et al, 2019).

Organismos bioindicadores são comumente usados para estudar mudanças na qualidade ambiental e na estrutura da paisagem (Ghannem et al, 2017). Os besouros da subfamília Scarabaeinae, conhecidos como escaravelhos ou rola-bostas, são considerados excelentes bioindicadores por serem sensíveis às mudanças no ambiente, temperatura, umidade e cobertura do solo (Viegas et al, 2014; Gerlach et al, 2013; Noriega et al, 2020). Eles podem ser classificados em grupos funcionais de acordo com sua dieta (isto é, coprófago, necrófago, generalista), nidificação (ou seja, telecoprídeos, paracoprídeos e endocoprídeos) e biomassa corporal (Santos-Heredia et al., 2018. Carvalho et al., 2020). Os telecoprídeos (roladores) manipulam pequenos porções do recurso, que são transformadas em esferas e roladas para longe das fontes até que sejam enterrados no solo; paracoprídeos (cavadores) escavam túneis subterrâneos logo abaixo da fonte; endocoprídeos (residentes) se alimentam e nidificam diretamente na massa fecal (Halffter e Edmonds, 1982; Batilani, 2015). Através da manipulação, realocação e consumo de fezes de mamíferos por rola-bostas, uma série de funções ecológicas são desempenhadas por esses insetos. Entre essas funções, rola-bostas realizam ciclagem de nutrientes, supressão de parasitas, aeração do solo e dispersão secundária de sementes derramadas por mamíferos (Hanski et al., 1991; Nichols et al., 2009). A alta abundância de suas assembleias, a facilidade de coleta de espécimes e a taxonomia bem resolvida também suportam seu uso como ferramenta de monitoramento (Gardner et al, 2008). Além disso, o uso de grupos funcionais como ferramenta para uma avaliar o efeito das mudanças ambientais permite uma compreensão mais precisa da dinâmica ecológica, que pode ser mascarada por abordagens de escala mais ampla (por exemplo, estrutura de assembleia) (Melo et al, 2009).

A transformação das paisagens naturais, associados às atividades de desmatamento podem prejudicar a diversidade e o tamanho corporal de besouros rola-bosta (Sanchez-de-Jesus, 2016; Bitencourt et al, 2019; da Silva et al, 2019; Souza et al, 2020). Estas transformações vêm demonstrando uma clara relação de causa-consequência entre a quantidade de borda, de matrizes não florestadas e de cobertura florestal sobre a diversidade taxonômica e funcional dos rola-bostas. Estudos mostram que o aumento das áreas urbanas também limita a diversidade de rola-bostas, reduzindo a diversidade de grupos funcionais específicos (i.e. dieta e estratégia de remoção de recurso) (Braga et al, 2013; Ramírez-Restrepo e Halffter, 2016; Salomão et al, 2019). Além disso, as funções ecológicas dos rola-bostas estão diretamente relacionadas à diversidade, abundância e tamanho corporal das assembleias (Korasaki et al, 2013; Tonelli et al, 2018; Correa et al, 2019. É esperado que a diminuição da cobertura florestal nas paisagens urbanas da Amazônia diminua a riqueza, abundância e tamanho corporal de espécies de besouros rola-bosta. Também se espera que mesmo em cidades diferentes, fragmentos com estruturas similares compartilhem comunidades similares devido a estrutura do ambiente. Além disso, embora paisagens fragmentadas no Antropoceno possam conservar espécies nativas em ecossistemas não nativos (Arroyo-Rodríguez et al, 2020), espera-se que paisagens com maior número de manchas florestais (i.e. mais fragmentadas) e maior densidade de borda afetem negativamente a diversidade de besouros.

OBJETIVO

O objetivo geral deste estudo foi avaliar os efeitos da estrutura da paisagem sobre as assembleias de rola-bostas que habitam fragmentos florestais localizados em cidades da Amazônia Central. Especificamente, se analisou como a quantidade de cobertura florestal, cobertura agrícola, densidade de borda e o número de fragmentos florestais afetam a riqueza, abundância, composição de espécies e tamanho do corpo para toda a comunidade de besouros rola-bosta e por cada grupo funcional. Os efeitos da paisagem nas assembleias de besouros rola-bosta foram avaliados usando os dados totais e por grupos funcionais, objetivando a compreensão mais ampla e fina dos efeitos da urbanização. Os grupos funcionais foram divididos de acordo com a estratégia de remoção de recursos dos besouros (roladores, tuneleiros e residentes) e dieta (coprófagos, necrófagos e generalistas).

Capítulo 1

Mesquita, V.P.; Bernardino, G.V.S.; Bobrowiec, P.E.D.; Salomão, R.P.; Cornelius, C. How does landscape structure affect dung beetle assemblages in Amazon cities? Manuscrito em preparação para submissão para *Urban Ecosystems*.

How does landscape structure affect dung beetle assemblages in Amazon cities?

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ABSTRACT

In the world, the growth of cities is one of the main direct and indirect factors responsible for the loss of native vegetation cover. In the Amazon, landscape transformations related to urbanization have been causing the replacement of natural areas by urban landscapes. These changes directly affect the biological communities that reside in forest remnants inserted in cities, compromising the maintenance of urban and natural ecosystems. This work sought to understand how changes in the landscape affect assemblages and functional groups (i.e. diet and resource removal strategy) of dung beetles in cities in Central Amazonia. 38 urban forest fragments were analyzed in six municipalities belonging to the metropolitan region of Manaus, Amazonas. Among the landscape variables analysed (i.e. forest cover, agricultural area, edge density and number of patches around the fragment) forest cover was the most determining factor, negatively affecting species richness, abundance and general body size, and also the different functional groups (i.e. diet and resource removal strategy). Higher edge density positively affected the tunneller functional group. The largest number of fragments negatively affected the abundance of diet generalists, dweller richness and coprophagous body size. These results demonstrate that changes in ecological diversity caused by urbanization are driven by different landscape parameters, and each is exerting pressure on different aspects of assemblages. This study contributes to the understanding of how changes in the amount and distribution of forest cover in tropical cities affects the taxonomic diversity of dung beetles assemblages.

Keywords: Biotic homogenization, Community ecology, Rainforest, Scarabaeinae, Urban sprawl

INTRODUCTION

The change in land cover caused by the advance of urban areas is one of the main factors related to urbanization that impacts biodiversity (Muller et al, 2018). The accelerated growth of urban areas is linked to the processes of fragmentation of natural environments, generating forest remnants surrounded by a matrix composed mostly by impervious surfaces (Parris, 2016; Magura et al, 2020), incapable of being used by communities in forested environments. The growing human concentration in urban centers demands increases in the availability of energy, spaces and natural resources (Marzluff et al, 2001; Elmqvist et al, 2013). Through different land uses, human activities alter processes and the stability of natural ecosystems (Deng et al, 2021). Studies describe changes in the composition and structure of assemblages of species associated with the urban environment that directly affect biodiversity, leading to decreases in species richness, abundance and functional diversity (Violle et al, 2007; McKinney, 2008; Aronson et al, 2014). Furthermore, environmental disturbances caused by increased urbanization can result in loss or reduction of suitable habitat for native communities, introduction of exotic species and changes in habitat quality and food availability (McKinney, 2002; Kowarik, 2011).

In the Brazilian Amazon, urban areas evolved with the emergence of intermediate-sized cities and the multiplication of small urban centers, which follow the routes of the main highways and rivers in the region (Sathler et al, 2009). Despite being a region that has historically been altered by human activities (Macedo at al., 2021), the Amazon still has a large portion of native forest cover. In this sense, the non-urbanized regions of the Amazon present a relatively pristine condition, especially when compared to other tropical forests (Vitel et al, 2009, Levis et al, 2017). In addition to the incipient knowledge regarding the effects of urbanization on ecological diversity in the Amazon (Morris et al, 2010), the forest matrix that surrounds the cities of this ecosystem represents a unique scenario regarding the dynamics of urbanization in the tropics. Through knowledge about the effects of urbanization in cities in the Amazon, it is possible to deepen the understanding of the resilience of ecological communities in the face of abrupt changes in tropical landscapes.

To understand how the urbanization process affect communities, landscape ecology stands out as an optimal approach that helps to understand how the spatial organization of landscape units influence species distribution (Metzger, 2001). For example, in relatively untouched forest areas, the impact of urbanization may manifest itself differently from that of intensively managed agricultural land (Venugopal et al, 2012). With the increase of cities, much of the forest cover is converted into other types of land cover, through a fragmentation process that generates smaller native remnants isolated from each other by a urban matrix, which is highly distinct from the original (Laurance et al, 2000; 2009). Together with such changes, there is an increase in the density of edges surrounding the forest remnants embedded in cities, impacting the structure and composition of forests and its communities (Harper et al, 2005). Forest edges comprise an ecotone between a native and a non-native habitat, and higher edge densities results in larger forested areas that are suffering from the effects of the surrounding land use (e.g. high wind activity, temperatures, and light intensity, see Laurance, 1991). The environmental changes promoted by urban matrices in forest remnants can lead to greater vulnerability of these areas (McDonald et al, 2013). Therefore, such changes in biodiversity can directly imply in the provision of ecological services (e.g. food and raw material production, climate regulation, soil conservation and biodiversity) provided by native communities (Tolessa et al, 2017; Liu et al, 2019). Changes in land cover and landscape configuration lead to biotic homogenization in disturbed areas, which consists in increasing taxonomic, functional and genetic similarity between two or more communities over space and time (Dornelas et al, 2014; Bittencourt et al, 2019). By assessing the effects of landscape transformation due to urbanization, we can have cues regarding the best distribution of land uses that will allow a proper maintenance of the urban ecosystems.

Bioindicator organisms are commonly used to study changes in environmental quality and landscape structure (Ghannem et al, 2017). Among invertebrates, the dung beetles (Coleoptera: Scarabaeinae) are considered excellent bioindicators because they are sensitive to changes in the environment conditions, are highly diverse, and have a well-resolved taxonomy (Gardner et al, 2008; Viegas et al, 2014; Gerlach et al, 2013; Noriega et al, 2020.). They can be classified into functional groups according to their diet (ie, coprophagous, scavenger, generalist), resource removal strategy (ie, telecoprids, paracoprids, and endocoprids), and body biomass (Santos-Heredia et al., 2018. Carvalho et al. ., 2020). The telecoprids (rollers) manipulate small portions of the resource, which are formed into spheres and rolled away from the sources until they are buried in the ground; paracoprids (tunneller) dig underground tunnels just below the source; endocoprids (dweller) feed and nest directly in the fecal mass (Halffter and Edmonds, 1982; Batilani, 2015). Through manipulation, relocation and consumption of mammalian feces by dung beetles, a number of ecological functions are performed by these insects. Among these functions, dung beetles perform nutrient cycling, parasite suppression, soil aeration, and secondary dispersal of seeds shed by mammals (Hanski et al., 1991; Nichols et al., 2009). Moreover, the use of functional groups as a tool to assess the effect of environmental changes allows for a finer understanding of ecological dynamics, which may be masked by broader scale approaches (e.g. assemblage structure) (Melo et al, 2009). The use of functional groups has proven to be an important tool to understand the effects of environmental disturbances on biological communities, deciphering key dimensions of biodiversity in a clear, broad and predictive way (Podgaiski et al, 2011).

Previous studies suggest that the landscape effects associated to deforestation activities (e.g. increase of edge density and non-forested matrices, decrease of forest cover) can lead to a reduction on dung beetle biomass and diversity (Sanchez-de-Jesus, 2016; Bitencourt et al, 2019; da Silva et al, 2019; Souza et al, 2020). Considering the previous negative effects of urbanization on dung beetles in tropical ecosystems (Korasaki et al, 2013; Salomão et al, 2019; Correa et al, 2021a), the goal of this study was to evaluate the effects of landscape composition and configuration on the dung beetle assemblages that inhabit forest patches located in Amazon cities. Specifically, we tested how the amount of forest cover, agricultural cover, edge density, and the number of forest patches affect assemblage structure and similarities between dung beetles assemblages, as well as affects dung beetles species richness, abundance, species composition, and body size. For a finer assessment, landscape effects on dung beetle assemblages were analysed using both the whole data and for functional groups, according to beetles' resource removal strategy (rollers, tunnellers, and dwellers) and diet (coprophagous, necrophagous, and diet generalists). We expect that the decrease of forest cover in Amazonian urban forest fragmentswill decrease dung beetle species richness, abundance, and body size. Furthermore, although fragmented landscapes in the Anthropocene may conserve native species in non-native ecosystems (Arroyo-

Rodríguez et al, 2020), we expect that landscapes with a greater number of forest patches will negatively affect beetle diversity.

MATERIAL AND METHODS

Study area

The study was carried out in in the state of Amazon, Brazil, located in the urban and peri-urban areas of the cities of Iranduba, Itacoatiara, Manacapuru, Manaus, Presidente Figueiredo and Rio Preto da Eva (Fig. 1). City areas range from 2,216 km² to 25,459 km² (IBGE, 2022), and the number of inhabitants ranges from 34,856 to 2,255,903 (IBGE, 2021). According to the classification proposed by Köppen, the climate is humid tropical (Am), with an average annual rainfall of 2,286 mm and temperature varying between 27 and 29 °C (INMET, 2011). The rainy season in the region occurs between November and March (mean monthly rainfall: 299 mm), and the dry period occurs between May and September (mean monthly rainfall: 93 mm). Forest cover in our study fragmentss comprise mostly *terra firme* forest (i.e. ombrophilous tropical rainforest). The matrix in our studied fragmentss is composed mainly by urban cover, agricultural lands, and water cover. Surrounding urban fragmentss, the land cover comprises mostly primary and secondary forest, but also contains agriculture cover.

Data collection

We surveyed dung beetles between March and June 2021, at the end of the rainy period. We sampled beetles in 38 urban forest fragments (6 fragmentss per city, except for Manaus, in which we sampled 8 fragments, see Fig. 1) with sampling sites within forested areas. To capture the dung beetles, we used pitfall traps. Traps consisted of of a cylindrical plastic container (500 ml) buried at the ground level in the soil, with a small bait-holding recipient installed. Inside the cylindrical plastic container, we used 250 ml of a solution containing salt and detergent to kill and preserve the collected beetles. To attract the dung beetles, traps were baited with ca. 25 g of human excrement or ca. 25 g of carrion (decaying bovine liver). In each sampling site, 10 paired traps baited with excrement and carrion (in each pair, traps spaced 10 m between them) were installed each 25 m across a 250 m-long linear transect. The beetles that fell in traps were collected 48 h after the installation of the pitfall traps. A total of 760 traps (20 traps × 38 fragments) were installed in this study.

Determination of functional groups and estimation of species' body size

We identified beetles at species level with aid of taxonomic keys (Genier et al, 2009; Edmonds and Zidek, 2010; Vaz-de-Mello et al, 2011; Cupello and Vaz-de-Mello, 2019; Nazar-Silva and Silva, 2021), taxonomic experts (Dr. Mario Cupello), and reference material of the Entomological Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA). To determine species diet, we considered coprophagous or necrophagous species whenever more than 80% of their individuals were collected in excrement or carrion (see Halffter and Arellano, 2002). Species with less than 80% of their individuals collected in one of the resource types were classified as diet-generalist. We determined species diet for those with $n \geq 5$ captured individuals. Furthermore, dung beetles were classified in three groups according to their resource removal strategies: telecoprids (rollers) – manipulate small portions of the resource, which are transformed into small balls and rolled away from the sources and buried in the ground; paracoprids (tunnellers) – dig underground tunnels below the source; and endocoprids (dwellers) – feed and nest directly in the fecal mass (Halffter and Edmonds, 1982; Batilani, 2015). To estimate species' body size, we randomly used 30 beetles of each species and measured the larger pronotum width using digital images obtained from using a Samsung M32 digital camera under a microscope (Opton TIM-2B). We analyzed in ImajeJ software version 1.46r. All measurements were performed by VPM. The collected material was deposited in the entomological collections of INPA and the Universidade Federal do Mato Grosso (UFMT).

Landscape metrics

Landscape cover variables were obtained from a categorical land-cover map (MapBiomas Project – 2017 Collection). The MapBiomas Amazon project is an initiative to contribute to the understanding of the transformations occurring in the Amazon territory through the annual mapping of land cover and land use in the Amazon territory, making the data freely available (Souza et al, 2020). The MapBiomas project classifies and geo-references landcovers using LANDSAT data for all Brazilian biomes at a 30-m resolution with 95.9% accuracy level using an automatic classification routine (https://mapbiomas.org/analise-de-acuracia).

We quantified variables that describe the composition and configuration in each fragment: amount of forest cover (old-growth and/or secondary vegetation in different stages of regeneration), urban, agriculture, pasture, and water cover, number of forest patches, and edge density (for the forest class). We selected five different spatial scales (within a buffer radius of 200, 400, 600, 800, and 1,000 m centered in each sampling site), to achieve cover maximum home range size of beetle species (Cultid-Medina et al, 2015; Barretto et al, 2021; Salomão et al, 2021). We used QGIS 3.20.1-Odense software (QGIS, 2021) to obtain the amount of landscape cover for each sampling site at the different scales and the package *landscapemetrics*, a R package for calculating landscape metrics for categorical landscape patterns in R software (Hesselbarth et al 2019). Agriculture and pasture cover variables were grouped into the same cover (hereafter agriculture-pasture cover class), and water cover was not considered since this land cover category was present only in three fragments sampled.

Data analysis

As a first step we estimated landscape variables at different scales to ensure a good estimate of species-landscape relationships (Jackson & Fahrig 2015). Following this approach, we selected the spatial scale (circular buffers with 200, 400, 600, 800, and 1,000 m of radius) that best explained the variation of our response variables (species richness, abundance, and body size). The selection of models was based on the Akaike's Information Criterion corrected for small sample size (AICc). For each response variable, we performed models with different scales of the explanatory variables and family distributions (Gaussian, Poisson or Negative Binomial), and these models were ranked by their AICc. The best model (with the lowest AICc) among the competing models indicated the best scale of response for each predictor variable and the family distribution that best fitted the data distribution (see details of selected models in Table 1 of Supplementary Material).

We used Generalized Linear Mixed Models (GLMMs) to analyze the effects of landscape variables (i.e. forest, urban, and agriculture-pasture cover, edge density, and number of patches) on dung beetles species richness, abundance, and body size. Body size per fragmentscomprised the average of species body size calculated for the species obtained in eachfragment. Data were analyzed considering the entire community and each functional group (according to resource removal strategy and diet) separately. We constructed GLMM models with multiple landscape variables; each at the scale of best response. The models incorporated the cities as random effects to account for potential spatial autocorrelations between sites within the same city. Before constructing the models, we tested multicollinearity among the landscape cover variables, using VIFcor function of usdm package (Naimi, 2017). Forest cover and urban cover presented a high collinearity ($R^2 > 0.75$) and thus we excluded urban cover from all models. We constructed a full model containing all landscape variables and models with a subset of landscape metrics. The selection of models was based on the predictor variables rank based on the P-value. When there was a significant difference between the models ($P < 0.05$), the one with the lowest AIC was selected (Zuur et al, 2009). When there was no difference between the models, the most parsimonious model (the one with less variables) was selected. Analyses were performed using R software version 4.1.2 (R Development Core Team, 2022), and models were performed with the glmmTMB package (Brooks et al, 2017).

To analyze how forest cover, agriculture-pasture cover, edge density and number of patches affect dung beetle assemblage structure, we performed the Permutational Multivariate Analysis of Variance (PERMANOVA) using Bray-Curtis dissimilarity index vegan package (Oknasen et al, 2019). Bray-Curtis similarity index is sensitive to both species occurrence (i.e. species presence and absence) and species abundance. Assemblage structure was assessed for the whole assemblage and for functional groups according to the removal resource strategy (rollers, tunnellers, dwellers) and diet (coprophagous, necrophagous, diet-generalists). We estimated the PERMANOVA significance running 9999 permutations. The PERMANOVAs were run in vegan package (Oksanen, 2019). Dweller, necrophagous and diet-generalist beetles had not enough samplings, and thus were not analyzed in PERMANOVA (Table 3). We also performed similarity profile tests (SIMPROF) to explore the similarity in the dung beetle assemblage structure among the 38 studied fragments. SIMPROF was performed following Bray-Curtis similarity index. This approach form cluster of samples (in our study, each sample was considered one landscape) and assess the statistical difference among the different clusters. Since forest cover at 600m scale was the one that best explained shifts in dung beetle diversity (see Results section bellow), we included such variable in each sample unit (i.e. the 38 studied fragments) of the SIMPROF results. SIMPROF was conducted with Primer software version 6.0 (Clarke and Gorley, 2006).

RESULTS

A total of 5,576 dung beetles from 15 genera and 55 species were collected in the sampled fragments (Table 1). *Canthon* and *Dichotomius* were the most diverse genera, with 8 and 7 species recorded, respectively, while *Pseudocanthon*, *Phanaeus*, and *Scybalocanthon* were the least diverse genera, each one comprising two or one species. *Deltochilum submetallicum* (Castelnau, 1840), *Deltochilum aspericolle* (Bates, 1870) and *Canthon triangularis* (Drury, 1770) were the dominant species, together corresponding to 28% of the total abundance. In addition, these species were the most widespread, being recorded in 27 (*D. submetallicum*), 26 (*D. aspericolle*), and 22 (*C. triangularis*) of the 38 fragments (Supplementary material S1). Species richness per city ranged from 36 to 28 species, being Manaus the most speciose city and Itacoatiara the least speciose one (Table 1). Regarding species abundance per city, Iranduba was the most abundant city (n = 1,295), while Rio Preto da Eva was the least abundant (n = 531).

Regarding beetles' body size, *Coprophanaeus lancifer* (Linnaeus, 1767), *Coprophanaeus jasius* (Olivier, 1789) and *Dichotomius worontzowi* (Pereira, 1942) were the largest species, measuring 33.7, 28.9, and 21.9 mm, respectively, while *Uroxys* sp1, *Canthidium* sp2, *Uroxys* sp4, and were the smallest ones (respectively measuring 0.28, 0.26 and 0.22 mm, see Table 1). A total of 4,378 beetles from 54 species were collected in excrement-baited traps and 1,198 beetles from 37 species were collected in carrion-baited pitfall traps. Regarding beetle diet, 36 species were classified as coprophagous, two as necrophagous (*D. aspericolle, C. jasius)*, and two as diet-generalists (*D. submetallicum, Deltochilum granulatum*). When considering resource removal strategies, most of the species were tunnellers (31 species; 2,825 individuals), followed by rollers (18; 2,526), being dwellers the least speciose (s = 6) and abundant (n = 225) group (Table 1).

Forest cover was the most determinant landscape metric, affecting beetle species richness, abundance, and body size of the whole data, as well as for the different functional groups (Table 2). The increase of forest cover positively affected total species richness, abundance, and body size (Fig. 2A-C). Regarding resource removal strategies, almost all groups were positively affected by the increase of forest cover (Fig. 2D-I), except for tunneller abundance, roller, and dweller body size, which were not affected by the changes in the amount of forest cover. According to dung beetle diet, there was a positive effect of forest cover on their species richness, abundance, and body size for all diets (Fig. 2J-P). Nonetheless, the abundance of coprophagous species richness and the body size of diet-generalist species were not related to the any landscape metric (Table 2). Only tunneller dung beetles were affected by edge density, which positively affected theirspecies richness and species abundance (Fig. 3A-B). Finally, the increase in the number of forest patches negatively affected the dweller species richness (Fig. 4A), abundance of diet-generalist beetles (Fig. 4B) and coprophagous body size (Fig. 4C).

Forest cover was the only driver of differences in the dung beetle assemblage structure (Table 3). Since forest cover at 600m scale was the one that best explained shifts in dung beetle diversity, the whole dung beetle assemblage was influenced by forest cover. Among the functional groups comprising resource removal strategies, tunnellers and rollers were influenced by forest cover. Nevertheless, when considering beetles' diet, only coprophagous beetles were influenced by forest cover. Assemblage structure clustered dung beetles into eight significantly distinct groups (Fig. 5). One group comprised fragmentss with low amount of forest cover from the two largest cities, Manaus (fragments with 33 and 40 ha of forest cover at 600m buffer scale) and Itacoatiara (20 ha of forest cover at 600m buffer scale), clustering together with 17% similarity (Fig. 5A). The same was observed for fragmentss with high amounts of forest cover from different cities, comprising clusters from Manaus and Itacoatiara (25% similarity among such fragments, Fig. 5B), Rio Preto da Eva, Presidente Figueiredo, and Manaus (52%, Fig. 5C), Iranduba (62%, Fig. 5E), and Manacapuru (58%, Fig. 5F). The largest cluster (comprising 8 of the 38 studied fragments) grouped the fragmentss with the lowest amounts of forest cover (with minimum of 12 ha and maximum 76 ha at 600m buffer scale) from four of the six studied cities (Rio Preto da Eva, Manaus, Presidente Figueiredo and Manacapuru, Fig. 5H), clustering together with 12% similarity.

DISCUSSION

The expansion of urban centers causes marked changes in the structure and composition of the urban forest fragments, challenging the maintenance of biodiversity in cities (Faeth et., 2011). In the Amazon cities of our study region, urban expansion had a relevant increase since the 80s, which was followed by environmental shifts in natural and semi-natural ecosystems (Browder, 2002; Chaves et al, 2020). The observed shifts in land-use due to urbanization in this region, which is one of the most urbanized in Amazon (Barbieri et al, 2007; Chaves et al, 2020), are determinant for dung beetle assemblages. Among the results of this study, we emphasize that (1) forest cover was the main driver of shifts on dung beetle assemblage, while (2) edge density and number of patches affected specific functional groups. These results show that shifts on ecological diversity caused by urbanization process is driven by different landscape parameters, and each one is exerting pressure on different aspects of ecological assemblages. This study contributes to the understanding of how the change in the amount and distribution of forest cover in tropical cities affect the taxonomic diversity of dung beetles.

As observed in other taxonomic groupss (Seress & Liker, 2015; Hantak et al, 2021), forest cover was determinant for maintaining dung beetles biodiversity in urban landscapes. The loss of forest cover was the variable that most affected dung beetle assemblage structure, decreasing species richness, abundance, and body size of the whole group and of the different functional groups. In urban ecosystems, even small forest patches can act as a refuge for many forest-dwelling species, while the urbanized non-habitat matrix surrounding forest patches strongly limit their distribution and diversity (Korasaki et al, 2013; Kang et al, 2015; Zungu et al, 2020; Correa et al, 2021a). With the decrease of forest cover, there is a strong effect of the environmental conditions from the surrounding ecosystems towards the forest interior (Alvarado et al, 2018). The environmental conditions offered by the urban matrix impair the distribution of forest-dwelling species (McKinney, 2002, 2008), but also the abundance and the size of individuals and species. Our results reinforce the results of previous studies (Nichols et al, 2007; Barragán et al, 2011; Ramírez-Restrepo et al, 2016; Correa et al, 2021b), indicating that disturbances caused by the urban matrix impair the structure of dung beetle assemblages.

The data presented in this study highlight a new and alarming scenario regarding urbanization in the tropics, with a marked impoverishment and filtering of dung beetle assemblages in Amazonian urban landscapes. According to our data, there is a deeply limited niche availability for dung beetles in urban landscapes with low amounts of forest cover, resulting in a decrease of species richness in more urbanized sites. Moreover, the decrease of abundance and body size with the decrease of forest cover indicates that there is a limited availability and quality of food resources, which are key parameters that impairs the establishment of higher abundances and large-bodied individuals (Nichols et al, 2009; Zanette at al., 2000). The loss of forest cover in urban areas is associated with the disappearance of mammals (McKinney, 2008; Villaseñor et al, 2014), which in turn have a direct relationship as resource providers for the dung beetles (Nichols et al, 2009). This study presents an alarming scenario, indicating that the urbanization dynamics in Amazon are resulting in oversimplified assemblages, which directly will impact the ecosystem services provided by such insects and consequently the environmental stability in cities.

Interestingly, the negative response of biodiversity to decrease of forest cover in urban areas of Amazon is contrasting with previous research conduced in neighboring tropical rainforests. In the Atlantic rainforest, located in almost the entire Brazilian coast, the decrease of forest cover in a city (João Pessoa, *ca.* 1,000,000 inhabitants) only affected specific subgroups of the dung beetle assemblage (Salomão et al, 2019). However, in the present study the decrease of forest cover had a general negative effect over beetle assemblage. We believe the João Pessoa dung beetle assemblages might be composed by generalist species, while the assemblages of the studied cities may still present more sensitive species. It has been suggested that ecosystems that are more pristine maintain ecological communities that are more sensitive to land-use transformation compared to those that have been suffering from strong and chronic anthropogenic activities (Tocher, 1998; Melo et al, 2013). In Brazil, the Atlantic rainforest has been undergoing an intense process of deforestation and urbanization since the beginning of the 16th century, and currently there are only *ca.* 12% of the original vegetation (de Santana et al, 2007; Ribeiro et al, 2011). In comparison, the Amazon has been experiencing a later process of modification of natural areas that began in the 1980s with the arrival of the first industries and the strong *rural exodus* that led to a rapid and disorderly growth of cities (Barbieri, 2009). Agricultural frontier development and deforestation in the Amazon follows the path of accelerated industrialization begun in the 1950s and amplified in Brazil's attempts to adapt to economic globalization. (Vieira et al, 2008). In addition, the matrix that intersperses the Amazonian cities is mainly composed of forest areas, contrasting to the agricultural monoculture matrices that dominate other tropical ecosystems. Our results together with previous studies may indicate that urbanization effects on biodiversity in tropics are context dependent. We reinforce the findings presented by Sanchez-de-Jesus et al. (2016), which suggests that Amazon communities tend to be more sensitive to anthropogenic threats compared to communities of other tropical ecosystems.

Contrary to our expectations, fragments with higher amounts of edge supported higher species richness and abundance of tunneller dung beetles. Commonly, the edge restrains the distribution of ecological assemblages that dwell in closed-forested environments (Zhen-Min and Guang-Zhi, 2000), which has been also observed for dung beetles (Souza et al, 2020). These studies suggest that negative ecological effects are due to the dissimilarity between forest and surrounding matrix and to the differences of habitat temperature. Considering the urban matrix, it seems that this environment is much more inhospitable for native species than non-urban ones (e.g. plantations, livestock). In the fragments with the greatest density of edges, the species that most occurred among the tunneller group were *Canthidium* sp4, *Coprophaneus jasius* (Olivier, 1789) and *Dichotomius lucasi* (Harold, 1869). Despite the adverse conditions provided in fragments with high edge density, the greater abundance of these species may be related to the availability of environmental conditions established near the urban matrix. Cities may have lower overall species diversity and abundance, but generalist species biomass and even diversity may be higher in these spaces. In addition, it is important to consider that the abrupt edges established by urban fragments limit the distribution of most species. Limiting environments establish niches that are barely used by native assemblages (Zanette et al, 2000). Among the abundant genera observed in fragments with high density of edges, *Dichotomius* comprise species that are often abundant in non-native conditions (Hernandez et al, 2009). *Dichotomius lucasi*, *C. jasius*, and *Canthidium* species are widely distributed and highly abundant in native and non-native habitats in Amazonian region (Scheffler et al, 2005).

Anthropogenic activities, including the urban establishment and expansion, triggers forest fragmentation (Fahrig, 2003), which in turn lead to an increase in the number of forest patches in cities where forest highlighted as the original native land cover. We found that the increase in the number of patches negatively affected diet-generalists' abundance, dwellers' species richness, and coprophagous' body size. The small new habitats provided by urban patches comprise ecological niches in which many species cannot persist (Li et al, 2017). The increase in the number of patches represents more fragmented landscapes and a limiting dispersal barrier for many species, including the dung beetles (da Silva et al, 2019). Moreover, in urban forest fragments it is common the entry of exotic species that can cause negative effects on wild mammals (i.e. main food providers for dung beetles), and consequently on dung beetles (Nichols, 2009; Mella-Mendez et al, 2019; 2015). Nonetheless, it is important to analyse our results with care, since the effects of the number of patches did not affect the whole assemblage, but only specific functional groups. In other words, we observed cues indicating limiting environmental conditions for diet-generalists (resulting in a decrease of their abundances), niche availability for dweller species (which limits their species richness) and decrease in food availability and habitat quality (variables related to species body size) for coprophagous species. Our data shows that the local imbalances and fragment quality lossprovided by the increase of habitat fragmentation in cities have different effects on the structure of dung beetle assemblages. It is important to carefully analyze the consequences of urban forest fragmentation on the above-mentioned functional groups to determine the key aspects that allow the maintenance of healthy urban assemblages. The complex set of effects related to forest fragmentation in this study reinforces the idea that different processes are co-occurring and are determinant for the maintenance of the biological diversity in cities.

Urbanization is a process that have well-known negative consequences to biodiversity (e.g. Elmqvist et al, 2013). Through this study, we provided important cues indicating that landscape structure and composition strongly determines dung beetle diversity in cities located in Amazon, the largest tropical rainforest in the world. Although forest cover featured as the most importance driving force of dung beetle assemblage, the density of edges and number of patches also comprised fundamental landscape attributes. With the loss of forest cover, the decrease of beetles' body size and abundance directly affect ecological functions performed by them, such as nutrient cycling and soil aeration (Larsen et al, 2005; 2008; Horgan, 2008; Nichols et al, 2008). The high sensitiveness of Amazonian beetle assemblages to urbanization process when compared to other tropical ecosystems (e.g. Salomão et al, 2019; Correa et al, 2021b) suggest that cities' effect on biodiversity can be ecosystem dependent. Future studies should focus on disentangling the role that ecosystem history plays in the urbanization effects on biodiversity.

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FIGURES

Figure 1. Map showing the location of the 38 fragmentsin the state of Amazon, Brazil. Each red point represents a study site. Figure obtained from Bernardino (2022).

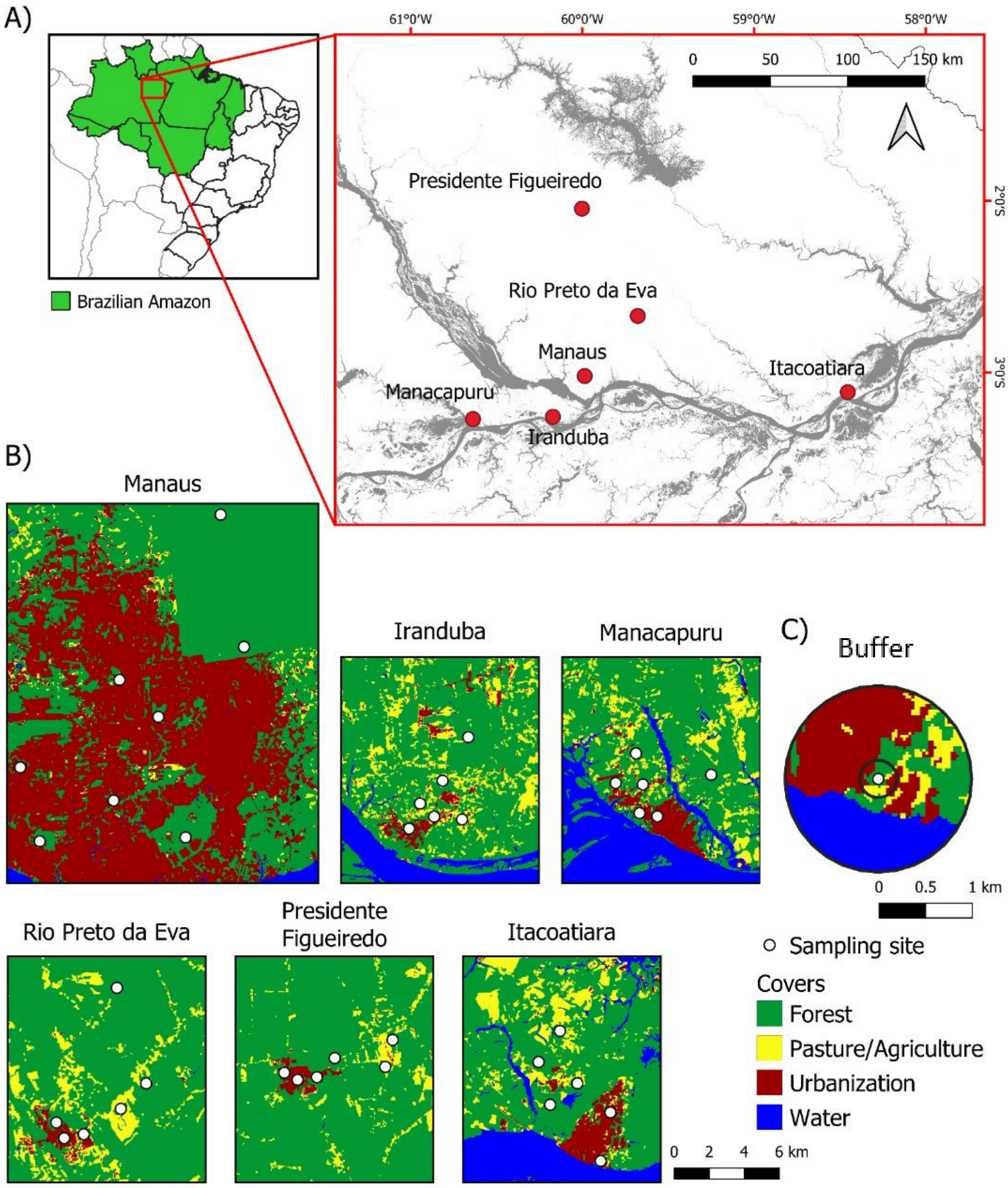


Figure 2. Linear regressions showing the statistically significant relationship between forest cover and dung beetle diversity species richness, abundance, and body size.

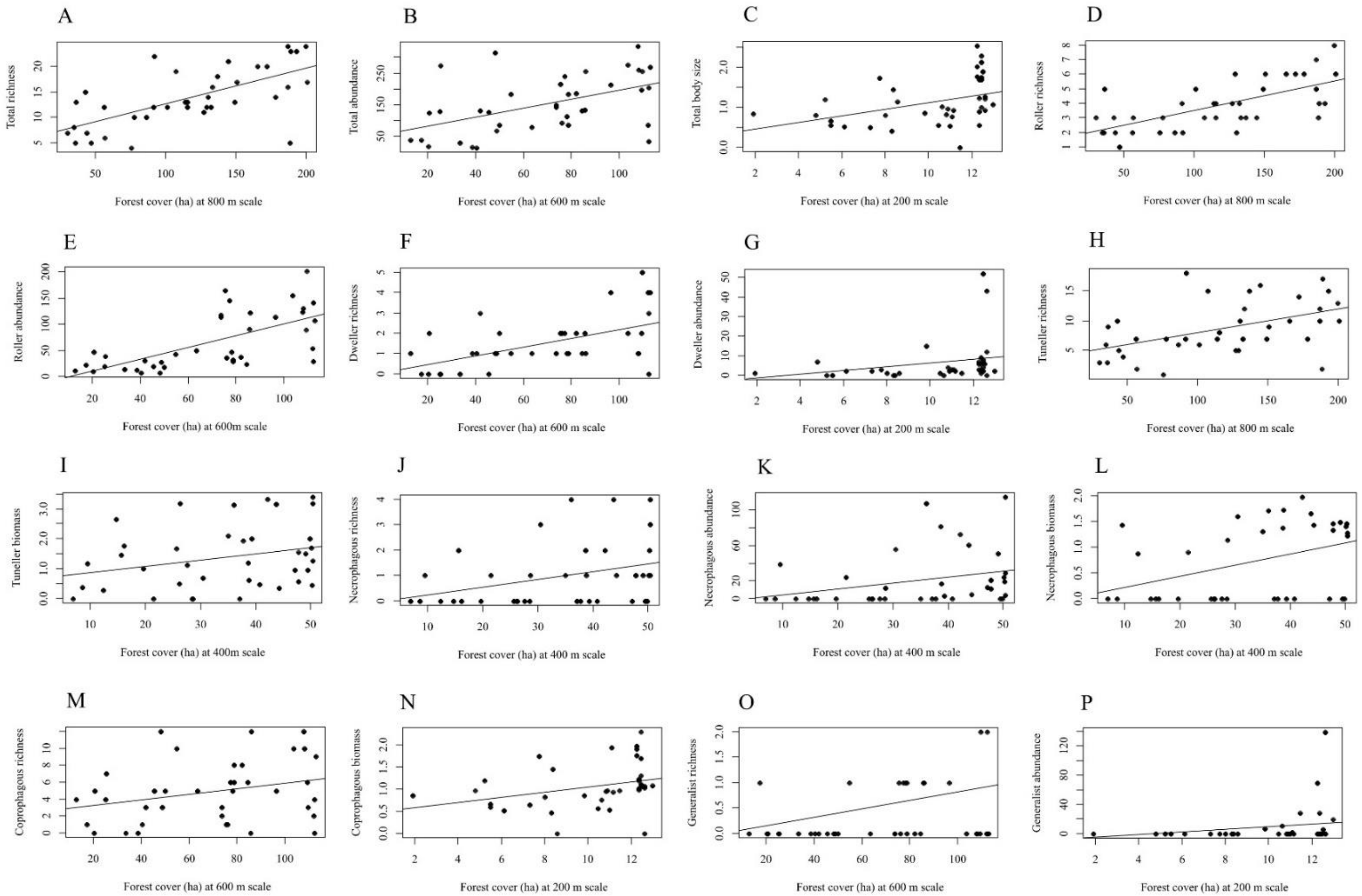


Figure 3. Statistically significant relationship between the edge density and tunneller abundance (A) and species richness (B).

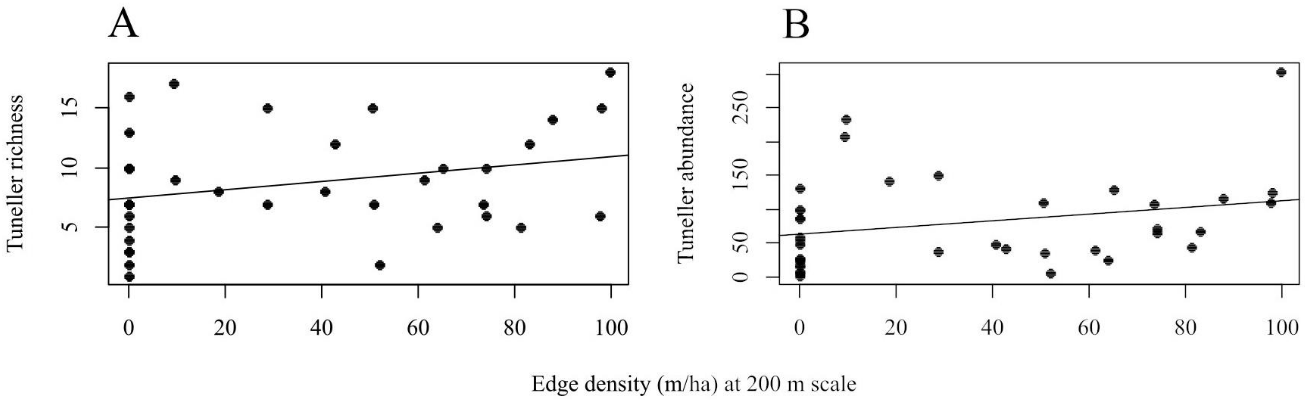


Figure 4. Linear regressions showing the relationship between number of patches and diet-generalist abundance (A), dwellers species richness (B), and coprophagous body size (C).

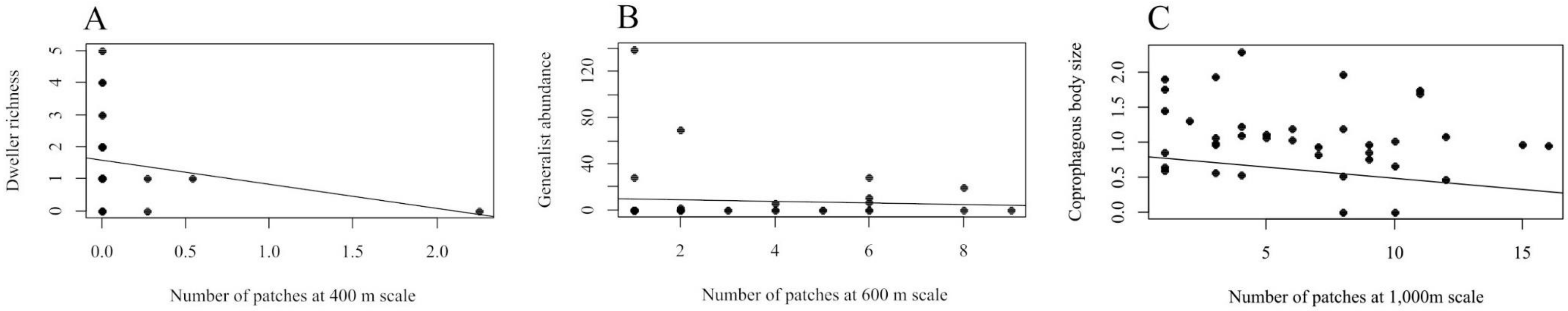
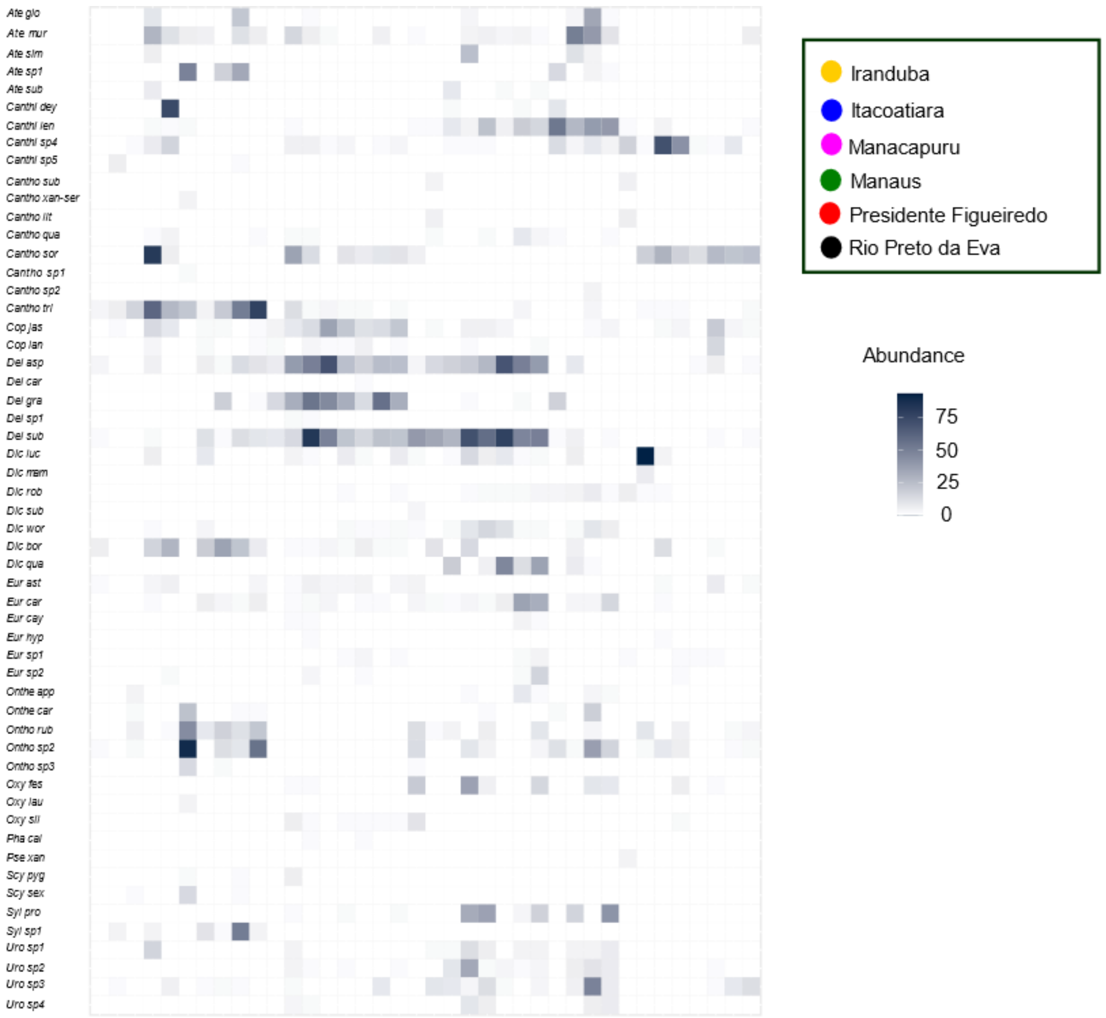


Figure 5. Heatmap showing species distribution of dung beetles recorded in the 38 urban landscapes in six Amazonian cities at 600m buffer scale. Dendrograms of group-averaged clustering dung beetles and sampling sites using Bray-Curtis similarity index. Dashed lines represent statistical differences between groups (statistically significant groupings were presented by letters), based on SIMPROF analyses.


Ate glo
Ate mur
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Canthi len
Canthi sp4
Canthi sp5
Cantho sub
Cantho xan-ser
Cantho lit
Cantho qua
Cantho sor
Cantho sp1
Cantho sp2
Cantho tri
Cop jas
Cop lan
Del asp
Del car
Del gra
Del sp1
Del sub
Dic luc
Dic mam
Dic rob
Dic sub
Dic wor
Dic bor
Dic qua
Eur ast
Eur car
Eur cay
Eur hyp
Eur sp1
Eur sp2
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Onthe car
Ontho rub
Ontho sp2
Ontho sp3
Oxy fes
Oxy lau
Oxy sil
Pha cal
Pse xan
Scy pyg
Scy sex
Syl pro
Syl sp1
Uro sp1
Uro sp2
Uro sp3
Uro sp4
Iranduba
Itacoatiara
Manacapuru
Manaus
Presidente Figueiredo
Rio Preto da Eva
Abundance
75
50
25
0

Table 1. Dung beetle species list recorded in pitfall traps baited with carrion or excrement in six cities of Amazonas state, Brazil. Tun – tunneller; Rol – roller; Dwe – dweller; Tun – tunneller; Cop – coprophagous; Nec – necrophagous; Gen – diet generalist; NA – unavailable data.

Species	Body size (mm)	Resource removal Strategy	Diet	Iranduba	Itacoatiara	Manacapuru	Manaus	Presidente Figueiredo	Rio Preto da Eva	Total
Ateuchus sp1	4.9	Tun	Cop	19	98	0	0	0	0	117
Ateuchus globulus	6.5	Tun	Cop	41	21	0	9	1	0	72
Ateuchus murrayi	5.0	Tun	Cop	108	28	8	39	15	21	219
Ateuchus simplex	4.1	Tun	Cop	39	0	0	6	0	0	45
Ateuchus substriatum	6.3	Tun	Cop	0	0	12	7	0	0	19
Canthidium deyrollei	3.9	Tun	Cop	9	0	4	73	0	0	86
Canthidium gr *lentum*	4.7	Tun	Cop	184	2	49	7	1	2	245
Canthidium sp2	2.6	Tun	Cop	0	7	0	0	0	0	7
Canthidium sp4	6.2	Tun	Cop	30	0	18	95	52	19	214
Canthon subcyanaeus	5.6	Rol	Cop	0	0	9	0	0	0	9

Species	Body size (mm)	Resource removal Strategy	Diet	Iranduba	Itacoatiara	Manacapuru	Manaus	Presidente Figueiredo	Rio Preto da Eva	Total
Canthon gr *xanthopus-sericatus*	6.7	Rol	Cop	0	4	0	0	0	0	4
Canthon lituratus	5.6	Rol	Cop	0	0	11	0	0	0	11
Canthon quadriguttatus	5.0	Rol	Cop	4	1	13	5	2	2	27
Canthon sordidus	8.1	Rol	Nec	0	0	0	141	44	129	314
Canthon sp1	NA	Rol	NA	0	2	0	0	0	0	2
Canthon sp2	NA	Rol	Cop	4	0	0	0	0	0	4
Canthon triangularis	13.1	Rol	Cop	3	181	3	110	7	16	320
Coprophaneus jasius	28	Tun	Nec	14	6	5	39	78	54	196
Coprophaneus lancifer	33.7	Tun	COP	1	3	2	10	5	16	37
Deltochilum aspericolle	7.8	Rol	Nec	55	31	186	32	216	70	590
Deltochilum carinatum	NA	Rol	NA	0	0	0	1	0	0	1
Deltochilum granulatum	8.4	Rol	Gen	18	19	2	27	173	63	302

Species	Body size (mm)	Resource removal Strategy	Diet	Iranduba	Itacoatiara	Manacapuru	Manaus	Presidente Figueiredo	Rio Preto da Eva	Total
Deltochilum sp1	NA	Rol	Cop	0	0	0	0	1	2	3
Deltochilum submetallicum	7.5	Rol	Gen	134	33	235	26	221	38	687
Dichotomius lucasi	15.8	Tun	Cop	26	8	12	105	3	11	165
Dichotomius mamillatus	24.1	Tun	NA	0	0	0	7	0	0	7
Dichotomius robustus	21.6	Tun	COP	18	0	13	2	0	1	34
Dichotomius subanaeus	NA	Tun	NA	0	0	0	0	3	0	3
Dichotomius worontzowi	21.9	Tun	Cop	39	3	17	2	2	2	65
Dichotomius boreus	14.5	Tun	Cop	19	83	10	68	7	5	192
Dichotomius quadrilobatus	15.4	Tun	Cop	12	0	112	0	0	0	124
Eurysternus atrosericus	05.8	Dwe	Cop	0	3	0	15	13	13	44
Eurysternus caribaeus	15.2	Dwe	Cop	26	17	75	3	9	1	131
Eurysternus cayannensis	10.4	Dwe	Cop	0	0	5	0	1	1	7
Eurysternus hypocrita	NA	Dwe	NA	0	0	0	2	1	1	4

Species	Body size (mm)	Resource removal Strategy	Diet	Irandu ba	Itacoatiar a	Manacapu ru	Mana us	Presidente Figueiredo	Rio Preto da Eva	Total
Eurysternus sp1	7.6	Dwe	Cop	0	0	7	3	1	3	14
Eurysternus sp2	9.9	Dwe	Cop	0	0	19	3	4	0	26
Ontherus appendiculatus	11.6	Tun	Cop	6	0	9	4	0	0	19
Ontherus carinifrons	17.1	Tun	Cop	21	25	0	2	0	0	48
Onthophagus rubrescens	4.8	Tun	Cop	9	101	14	16	17	5	162
Onthophagus sp2	5.1	Tun	Cop	79	164	4	13	19	3	282
Onthophagus sp3	5.5	Tun	Cop	0	16	0	0	1	0	17
Oxysternon festivum	17.6	Tun	Cop	58	0	15	0	27	2	102
Oxysternon lautum	NA	Tun	NA	0	4	0	0	0	0	4
Oxysternon silenus	11.3	Tun	Cop	0	0	0	1	16	7	24
Phanaeus chalcomelas	NA	Tun	NA	0	0	0	1	1	0	2
Pseudocanthon xanthurus	NA	Rol	NA	0	0	4	0	0		4
Scybalocanthon pygidialis	5.2	Rol	Cop	0	3	0	0	0	6	9

Species	Body size (mm)	Resource removal Strategy	Diet	Iranduba	Itacoatiara	Manacapuru	Manaus	Presidente Figueiredo	Rio Preto da Eva	Total
Scybalocanthon sexpilotus	5.6	Rol	Cop	0	15	0	1	0	0	16
Sylvicanthon proseni	8.2	Rol	Cop	125	0	21	0	0	3	149
Sylvicanthon seag	6.6	Rol	Cop	0	70	0	4	0	0	74
Uroxys sp1	2.8	Tun	Cop	33	0	12	16	0	0	61
Uroxys sp2	2.8	Tun	Cop	58	0	16	0	0	1	75
Uroxys sp3	3.5	Tun	Cop	75	5	22	5	0	9	116
Uroxys sp4	2.2	Tun	Cop	28	0	0	0	0	2	30
Abundance				1300	951	898	941	956	530	
Species richness				31	28	32	36	33	30	

Table 2. Statistical models analyzing the effect of forest cover, agricultural cover, edge density, and number of patches on species richness, abundance and body size of dung beetles, analyzed according to total data, and for each species group (i.e. according to diet and resource removal strategy). Statistically significant effects are shown in bold. NA = variable not selected by the best supported model.

	Forest cover (%)		Spatial scale (*m*)	Agriculture cover (%)		Spatial scale (*m*)	Edge density (m/ha)		Spatial scale (*m*)	Number of patches		Spatial scale (*m*)	R2m	R2c	*Family*
	Z	P		*Z*	P		*Z*	P		*Z*	P				
Richness															
Total	0.069	<**0.01(+)**	800 m		NA			NA			NA		0.43	0.50	Gaussian
Roller	0.006	<**0.01(+)**	800m		NA			NA			NA		0.26	0.26	Poisson
Tunneller	0.004	<**0.01(+)**	800 m	-0.002	0.44	800 m	0.005	**0.06(+)**	200 m		0.59	1000 m	0.33	0.56	Poisson
Dweller	0.014	<**0.01(+)**	600 m		NA			NA		-0.23	**0.05(-)**	400 m	0.32	0.32	Poisson
Coprophagous	0.005	**0.03(+)**	600 m		NA		0.003	0.12	200 m		NA	200 m	0.14	0.62	Poisson
Necrophagous	0.070	<**0.01(+)**	400 m		NA			NA		-18.0	1.00	200 m	0.97	0.98	Poisson
Diet-generalist	0.012	<**0.01(+)**	1000 m		NA			NA			NA		0.20	0.20	Poisson
Abundance															
Total	0.011	<**0.01(+)**	600 m		NA		0.004	0.08	200 m		NA		0.76	1.00	Negative Binomial

	Forest cover (%)		Spatial scale (*m*)	Agriculture cover (%)		Spatial scale (*m*)	Edge density (m/ha)		Spatial scale (*m*)	Number of patches		Spatial scale (*m*)	R2m	R2c	*Family*
Roller	0.019	**<0.01(+)**	600 m		NA			NA			NA		0.81	1.00	Negative Binomial
Tunneller		NA	600 m		NA		0.006	**0.04(+)**	200 m		NA		0.29	1.00	Negative Binomial
Dweller	0.192	**0.01(+)**	200 m		NA			NA		-0.22	0.12	400 m	0.99	0.99	Negative Binomial
Coprophagous	0.006	NA	600 m		NA			NA			NA		0.15	1.00	Negative Binomial
Necrophagous	0.065	**<0.01(+)**	400 m		NA			NA		-17.65	1.00	200 m	0.98	1.00	Negative Binomial
Diet-generalist	0.668	**0.01(+)**	200 m		NA		0.033	0.14	600 m	0.28	**0.04(-)**	600 m	1.00	1.00	Negative Binomial
Body size															
Total	0.070	**0.03(+)**	200 m		NA		0.006	0.08	200 m	-0.05	0.08	800 m	0.22	0.22	Gaussian
Roller	0.168	0.23	200 m	-0.173	0.59	200 m	-0.004	0.67	200 m	-0.01	0.93	600 m	0.13	0.13	Poisson

	Forest cover (%)		Spatial scale (*m*)	Agriculture cover (%)		Spatial scale (*m*)	Edge density (m/ha)		Spatial scale (*m*)	Number of patches		Spatial scale (*m*)	R2m	R2c	*Family*
Tunneller	0.022	**0.06(+)**	200 m		NA			NA			NA		0.10	0.10	Poisson
Dweller		NA	400 m	0.178	0.34	200 m		NA			NA		0.02	0.02	Poisson
Coprophagous	0.057	**0.02(+)**	200 m		NA			NA		-0.11	**0.04(-)**	1000 m	0.19	0.29	Gaussian
Necrophagous	0.035	**0.03(+)**	400 m		NA			NA		-18.76	0.99	200 m	0.97	0.97	Poisson
Diet-generalist	0.008	NA			NA			NA			NA		0.93	0.93	Poisson

Table 3. Results from PERMANOVA analysis. Using forest cover, edge density and number of patches as predictor variables and dung beetle assemblage and functional groups by resource removal strategy and diet as dependent variable.

	Forest cover			Edge density			Number of patches		
	F	*P*	*R2*	*F*	*P*	*R2*	*F*	*P*	*R2*
Total	**4.04**	**0.0001**	**0.10**	0.90	0.54	0.02	0.88	0.57	0.02
Resource remouval strategy									
Roller	**5.12**	**0.0002**	**0.13**	0.41	0.92	0.01	0.92	0.49	0.02

Tunneller	**2.52**	**0.003**	**0.07**	0.89	0.57	0.02	1.02	0.42	0.03
Dweller	Low number of species per sampling site								
Diet									
Coprophagous	**3.43**	**0.0002**	**0.09**	0.98	0.45	0.03	0.98	0.47	0.03
Necrophagous	Low number of species per sampling site								
Diet-generalist	Low number of species per sampling site								

Supplementary material. Dung beetle species distribution, and landscape attributes in each sampling site studied.

CONCLUSÕES

Neste estudo, analisamos como as comunidades de besouros rola-bosta respondem à cobertura florestal em cidades da Amazônia. Nossos resultados mostram que as comunidades são holísticas à medida que a cobertura urbana aumenta. No entanto, mesmo em áreas altamente urbanizadas, paisagens com maior proteção protegida proporcionam uma comunidade mais equilibrada. Mesmo com o avanço do desmatamento e outras atividades antrópicas, a Amazônia ainda se destaca entre as florestas tropicais por possuir grandes porções de floresta intacta. Neste sentido, é necessário desenvolver estratégias que conciliem o crescimento urbano e a manutenção da biodiversidade deste ecossistema. Sugerimos que futuras pesquisas sobre urbanização na Amazônia e em outros biomas levem em consideração não apenas informações locais, mas também a história de urbanização das cidades e a matriz em que estão inseridas. Ressaltamos a importância de políticas públicas que visem o crescimento urbano de forma ordenada e planejada, comprometendo-se a preservar os espaços verdes já presentes nas cidades. Além disso, futuros estudos devem considerar a importância de parques, praças e corredores como elementos que possam favorecer a manutenção da biodiversidade e consequentemente a melhor qualidade de vida dos humanos.

CONCLUSIONS

In this study, we analyze how dung beetle communities respond to forest cover in cities in the Amazon. Our results show that communities are holistic as urban coverage increases. However, even in highly urbanized areas, landscapes with greater protected protection provide a more balanced community. Even with the advance of deforestation and other anthropic activities, the Amazon still stands out among the tropical forests for having large portions of intact forest. In this sense, it is necessary to develop strategies that reconcile urban growth and the maintenance of this ecosystem's biodiversity. We suggest that future research on urbanization in the Amazon and in other biomes considers not only local information, but also the urbanization history of cities and the matrix in which they are inserted. We emphasize the importance of public policies aimed at urban growth in an orderly and planned way, committing to preserve the green spaces already present in cities. In addition, future studies should consider the importance of parks, squares and corridors as elements that can favor the maintenance of biodiversity and, consequently, a better quality of life for humans.