UNIVERSIDADE FEDERAL DO OESTE DO PARÁ
INSTITUTO DE CIÊNCIAS E TECNOLOGIA DAS ÁGUAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BIODIVERSIDADE

MARIA KATIANE SOUSA COSTA

RESPOSTAS DAS ASSEMBLEIAS DE BESOUROS ESCARABEÍNEOS ÀS MUDANÇAS AMBIENTAIS E PRESENÇA DE SILVICULTURA NA AMAZÔNIA ORIENTAL

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Orientador: Prof. Dr. Rodrigo Ferreira Fadini
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Presidente

MARIA KATIANE SOUSA COSTA

Discente

A Deus, a luz que guia meus dias

A minha mãe Maria José, ao meu filho Lucas e ao meu esposo Renato, vocês são a razão de tudo. São minha força e determinação.

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É impossível chegar ao fim desse trabalho e não pensar em todas as pessoas que contribuíram para que eu chegasse até aqui. Agradeço primeiramente a Deus pois, sem Ele não somos capazes de superar os obstáculos que a vida nos impõe. Foi Deus que me fez ter a certeza de que estava no caminho certo e de que merecia tudo de bom que a vida tem a oferecer**.**

Agradeço à minha família por sempre me apoiar em todas as minhas decisões. Agradeço por todos os momentos de conflito em que estiveram ao meu lado, mesmo quando me faltou tempo para estar com vocês, e até mesmo pela paciência nos momentos mais estressantes. O amor e o apoio incondicional que vem se estendendo por toda a minha vida é o alicerce que sustenta meus sonhos e me permitem transformá-los em realidade. Em especial ao meu filho Lucas Eduardo, ao meu esposo Renato Vasconcelos e minha mãe, Maria José. Essa conquista é para vocês e por vocês, que sempre foram a razão pela qual eu busco novas oportunidades

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“Existem muitas hipóteses em ciência que estão erradas. Isso é perfeitamente aceitável, eles são a abertura para achar as que estão certas”. (Carl Sagan)

“A imaginação é mais importante que a ciência, porque a ciência é limitada, ao passo que a imaginação abrange o mundo inteiro”. (Albert Einstein)

RESUMO

Variáveis ambientais são importantes estruturantes das assembleias de besouros escarabeíneos na escala local em florestas preservadas no Neotrópico, mas qual a importância relativa dessas variáveis num contexto de mudança de uso da terra com o plantio de espécies florestais exóticas (i.e., eucalipto) adjacentes às florestas nativas não está claro. Neste estudo, perguntamos: [i] Como as assembleias de besouros serão influenciadas pela textura do solo, biomassa da serrapilheira, abertura do dossel e distância da silvicultura de eucalipto? E [ii] quais são as variáveis mais importantes para estruturar a composição de espécies de besouros? Para avaliar essas questões, utilizamos GLMs, regressões múltiplas multivariadas e análises de partição de variância hierárquica. A riqueza rarefeita de espécies de besouros diminuiu com o aumento da abertura do dossel e da porcentagem de areia do solo, mas apenas a distância da plantação de eucalipto, e não a textura do solo e a abertura do dossel, afetou significativamente a abundância de indivíduos de besouros A compreensão dos resultados desse estudo é importante num contexto de avanço do cultivo de espécies arbóreas exóticas, que vem se espalhando por várias regiões amazônicas nas últimas décadas, influenciando de uma maneira até então desconhecida a fauna do interior das florestas preservadas adjacentes.

Palavras-Chave: Brasil. Cobertura do dossel. Efeito de borda. Floresta de espécies exóticas Textura do solo.

ABSTRACT

Environmental variables are important for structuring dung-beetle assemblages in mature native forests the Neotropics at the local scale. However, their relative importance in the context of land-use changes with crops of exotic forest species (i.e., eucalyptus) close to native forests is still not clear. In this study we argue: [i] how are dung-beetles assemblages influenced by environmental variables (i.e., soil texture, litter biomass, canopy opening), and distance to eucalyptus plantations? and [ii] which are the most important variables for structuring dung-beetles species composition? In order to assess such issues, we used GLMs, multivariate multiple regression and hierarchical partitioning analysis. The rarefied species richness of beetle has decreased with the increase of canopy opening and the percentage of sand in the soil. However, the distance to eucalyptus plantation alone and not soil texture or canopy opening, has significantly affected beetle abundance. Understanding the results of this study is important in a context of expansion of exotic tree plantations, which has been spreading through several Amazonian regions in the last decades, thus influencing the native fauna within native preserved forests nearby.

Keywords: Brazil. Canopy cover. Edge effect. Exotic species forestry. Soil texture

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LISTA DE ABREVIATURAS E SIGLAS

Am	Clima tropical úmido
GLA	Gap Light Analyzer
GLM	General Linear Models
LECIN	Laboratório de Ecologia e Conservação de Invertebrados
PCoA	Principal Coordinate Analysis
PPBio	Programa de Pesquisa em Biodiversidade
PPGBEES	Programa de Pós-graduação em Biodiversidade
UFOPA	Universidade Federal do Oeste do Pará
VIF	Variance Inflation Factor

SUMÁRIO

1. INTRODUÇÃO GERAL

Proximidade com plantações de eucalipto afeta os besouros rola-bosta em florestas nativas primárias da Amazônia[1]

Qual o problema da pesquisa?

A subfamília Scarabaeinae é composta por besouros coprófagos mais conhecidos como rola-bosta, que apresentam ampla diversidade e distribuição geográfica. Desempenham um papel crucial em vários processos ecológicos contribuindo para a remoção de resíduos orgânicos e ciclagem de nutrientes, fertilização e aeração do solo, dispersão secundária de sementes e controle de parasitas de vertebrados. A maioria das espécies desse grupo apresenta forte associação com as variáveis ambientais que caracterizam seus habitats (estrutura do solo, abertura da copa das árvores, temperatura e umidade relativa), sendo altamente sensíveis às variações ocorrentes no ambiente

Os besouros rola-bosta vêm sendo amplamente utilizados em pesquisas ecológicas como um grupo bioindicador de mudanças ambientais, como nos processos de fragmentação florestal, de impactos causados pela mudança do uso da terra, além de fenômenos climáticos extremos e incêndios florestais. As mudanças no uso da terra e a degradação dos habitats naturais através do desmatamento, da fragmentação e da superexploração florestal são considerados as maiores ameaças à biodiversidade global. Um exemplo desse tipo de fragmentação é a substituição de imensas áreas de floresta nativa por monoculturas de eucaliptos . Essas atividades humanas promovem a substituição de ambientes heterogêneos por habitats mais simplificados e afetam negativamente a biodiversidade e suas funções ecológicas

A maioria dos estudos que avaliam a composição de espécies dos besouros rola-bosta identificam as características do habitat e da paisagem como muito importantes para determinar quais espécies, onde e quantos besouros serão encontrados. Outra questão é que em sua maioria são pesquisas comparativas entre tipos de vegetação muito diferentes (como pastos VS. florestas preservadas). Poucos estudos, no entanto, exploram como os besouros rola-bosta são influenciados colocar por mudanças sutis dentro do mesmo ambiente e da paisagem numa escala mais local, principalmente em áreas com gradientes ambientais pouco aparentes e paisagens dominadas por florestas plantadas com eucaliptos. Como será que essas florestas de eucalipto afetam os besouros que estão localizados nas florestas preservadas adjacentes?

Como a pesquisa foi realizada?

A pesquisa foi realizada na Jarí Florestal, localizada entre os estados do Pará e Amapá. Ela surgiu da necessidade de se conhecer a influência de diferentes características do habitat como a estrutura dosolo, abertura de dossel, profundidade da serrapilheira e da proximidade com a monocultura de eucalipto sobre o número de espécies, a quantidade de indivíduos, a biomassa (peso em gramas) e composição e estrutura das comunidades de besouros rola-bosta em florestas primárias não perturbadas da Amazônia (Figura 1). Nossas perguntas foram as seguintes: [1] Como as assembleias de besouros são influenciadas pelas características do habitat (estrutura dosolo, abertura de dossel, biomassa da serrapilheira) e pela proximidade com monocultura de eucalipto? E [2] quais são as características mais importantes para determinar mudanças na composição de espécies de besouros?

Figura 1. Espécies de besouros escarabeíneos encontrados na área de estudo.
Fotos: Filipe Machado França.

Coletamos informações dos besouros e das características do habitat em 34 locais, distribuídos dentro de uma área de floresta nativa primaria circundada por plantios de eucaliptos. Em cada local avaliamos o solo, a serapilheira, a abertura da copa das árvores e a distância até a plantação de eucalipto. Também instalamos armadilhas de queda do tipo *pittfal*, em que colocamos um porta-isca contendo fezes para atração e coleta dos besouros. A partir das informações coletadas em campo obtivemos um banco de dados que nos permitiu fazer inúmeras análises para identificar quais das características do habitat e da paisagem influenciam os besouros rola-bosta.

Qual a importância da pesquisa?

Os resultados deste estudo mostram que não só características do hábitat em florestas primárias influenciam na distribuição dos besouros rola-bosta, mas também características da paisagem, em específico, a distância até o plantio de eucalipto. Plantios com espécies florestais exóticas vêm se tornando cada vez mais comuns no Brasil e na Amazônia em particular, e seus efeitos sobre a fauna de florestas nativas precisam ser levados em consideração no planejamento para uso o adequado da terra.

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2. CAPÍTULO ÚNICO

Maria Katiane Sousa Costa, Filipe Machado França, Carlos Rodrigo Brocardo, Rodrigo Ferreira Fadini. (2022). Environmental variables and proximity to exotic tree plantations affect dung-beetles in forests with sandy soils in the Amazon. Manuscrito Submetido ao periódico Forest Ecology and Management. As normas indicadas para a redação de artigos pela revista estão disponíveis no link: https://www.elsevier.com/journals/forest-ecology-and-management/0378-1127/guide-for-authors

Environmental variables and proximity to exotic tree plantations drive dung beetle communities within Amazonian undisturbed forests

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ABSTRACT

Environmental variables are important for structuring dung-beetle assemblages in Neotropical forests. However, their relative importance in the context of land-use changes with crops of exotic forest species (i.e., *Eucalyptus* spp) close to native forests is still not clear. In this study we investigate [i] how dung beetle assemblages (i.e., rarefied species richness, biomass, abundance and species composition) respond to local environmental variables (i.e., soil texture, litter biomass, canopy opening) and proximity to eucalyptus plantations, and [ii] which metrics are the most important for structuring dung beetle assemblages We found that dung beetle species richness and abundance were higher in forests closer to *Eucalyptus* plantations, while rarefied species richness decreased with the increase of canopy opening and the percentage of sand in the soil. Our findings demonstrate the impacts of exotic tree plantations on the biodiversity of nearby native undisturbed forests, and are relevant when considering continuous expansion of exotic forest monocultures within tropical regions.

Keywords: Tropical forests, insect biodiversity, Edge effects, Exotic plantations, dung beetles.

2.1 Introduction

Habitat degradation and land-use changes are among the largest threats to global biodiversity (Dirzo and Raven, 2003; Morris, 2010). In the tropics, these disturbances are pushed mainly by the progress of monocultures and pastures (França et al. 2021) and by timber and non-timber resources exploitation within remaining forests (Barlow *et al*., 2016; Ceballos *et al*., 2015; Lewis and Maslin, 2015; Tabarelli *et al*., 2010). These human activities replace heterogeneous ecosystems with more simplified habitats, and negatively affect biodiversity and associated ecological functions (Braga *et al*., 2013; Correa *et al*., 2020, 2019; Martello *et al*., 2016).

Cultivating forest species for timber, cellulose, and coal production is a reality in several tropical countries. In the Amazon, for example, huge silviculture concessions started with rubber trees (*Hevea brasiliensis*), which replaced large areas of native forests in the early twentieth century (D'Agostini *et al*., 2013). As from the 1960's, two other monocultures expanded across the Amazon to meet the global timber and cellulose demands: eucalyptus (*Eucalyptus urugrandis*) and pine (*Pinus caribaea* var. *hondurensis*). The largest exotic plantations in the Brazilian Amazon are located in the states of Pará (~139,720 ha of eucalyptus), Amapá (62,880 ha of eucalyptus and 810 ha of pine), Mato Grosso (61,530 ha of eucalyptus and 10 ha of pine) and Tocantins (44,310 ha of eucalyptus and 850 ha of pine) (Pereira *et al*., 2010). However, the sustainable development of such practices is limited by the lack of knowledge about the impacts of these initiatives on tropical plant and animal biodiversity (Correa *et al*., 2016; Martello *et al*., 2018, 2016; Tavares *et al*., 2019).

The impact of silvicultural monocultures on biodiversity depends on multiple factors. For instance, planted forests with a structure similar to native forest environments can house biological communities similar to those found in undisturbed forests (Beiroz *et al*., 2017; Correa *et al*., 2020; Korasaki *et al*., 2013). However, although some species may benefit from landscapes with planted forests, others specialist species become extremely rare or locally extinct (Correa *et al*., 2016; Martello *et al*., 2018, 2016; Tavares *et al*., 2019; Vasconcelos *et al*., 2009). Bremes and Farley (2010), for example, have demonstrated that biodiversity in a *Eucalyptus* monoculture was influenced by the native forest proximity, local conditions, and landscape context. Nevertheless, little is known about the influence of exotic forest monocultures on the biodiversity of neighboring native forests, which could spread the land modification effect caused by exotic tree plantations beyond its boundaries.

Dung beetles (Coleoptera: Scarabaeinae) are largely used in ecological research due to their high sensitivity to environmental changes (Feer and Hingrat, 2005; Lopes *et al*., 2011; Silva *et al*., 2014; França et al. 2016). Most studies that assess the composition of dung beetle assemblages identify environmental and landscape variables as the most important drivers (Cottenie, 2005) for both most common and rare species (Silva and Hernández, 2016). For example, areas that preserve the largest forest coverage are normally richer in dung beetle species than areas with lower canopy cover (Giménez Gómez *et al*., 2018; Horgan, 2005).

Dung beetle diversity and biomass are markedly affected by environmental conditions of each ecosystem. Previous studies have demonstrated that the variation of clay concentration in the soil (Silva *et al*., 2014), amount of litter (Silva and Hernández, 2016), mammal defaunation (Cullot et al., 2013) and *Eucalyptus* monoculture planting (Barlow *et al*., 2007; Gardner *et al*., 2008) are important drivers of beetle diversity. For instance, tunneler dung beetles – i.e., species that bury their food resources immediately below or nearby the food resource – may have a disadvantage in clay soils (Griffiths *et al*., 2015; Salomão and Iannuzzi, 2015; Silva *et al*., 2015). Given their high sensitivity, dung beetles are widely used as indicators of environmental changes caused by forest fragmentation (Bitencourt and da Silva, 2016), land-use changes (França *et al*., 2018; Scheffler, 2005) and extreme climate events such as droughts and forest fires (França *et al*., 2020; Silveira *et al*., 2016). Besides, several studies indicate that dung beetles may respond to environmental variations similarly to other biological groups (Barlow *et al*., 2016; Edwards *et al*., 2011). Few studies, however, explore the way dung beetle communities are influenced by multiple local-scale microclimate conditions, particularly in Amazonian forests. Another issue is that most studies compare dung beetle communities between native and planted forests (Beiroz *et al*., 2017; Gardner *et al*., 2008; Silveira *et al*., 2010). Nonetheless, to our knowledge no previous work assessed how distance to *Eucalyptus* forests affect insect biodiversity within native undisturbed tropical forests.

To fill these knowledge gaps, our study assessed the influence of environmental variables (e.g. litter depth, soil structure, and canopy opening) and proximity to *Eucalyptus* monoculture on dung beetle species richness, abundance, biomass, and species composition within undisturbed primary forests in the Brazilian Amazon. Our research aims to answer the following questions: [i] how dung beetle assemblages respond to soil texture, litter biomass, canopy opening, and distance to eucalyptus plantations? and [ii] which predictors are the most important for structuring dung beetle assemblages? Our hypotheses are that [i] dung beetle abundance, species richness and biomass will increase in forests with a larger percentage of sand in the soil, lower canopy opening, and more distant to *Eucalyptus* plantations; and that [ii] the sand soil percentage will be the most important driver of dung beetle species composition.

2.2 Materials and methods

2.2.1 Study region

Our study was carried out at Jari Florestal, a large-scale tree plantation and timber forestry concession located in Almeirim, Pará state, in the northern portion of the Brazilian Amazon (0 ° 27′S 51 ° 40′W) (Fig. 1). Jari Florestal occupies an area of 1,259,958 ha, of which ~129,200 ha (9% of the total area) are *Eucalyptus* plantations while 545,000 ha are native forest planned to be or already selectively logged. According to Köppen’s classification, the region is under a tropical monsoon climate (Am) with a brief dry season (Andrade *et al*., 2017). The average mean temperature is 26.4°C, while annual precipitation is between 1998.2 and 2347.7 mm. Rainfall distribution is irregular throughout the year, with more rain between March and May and less rain between September and November (Sobrinho *et al*., 2012). Most soils in the region are rich in clay (Batista and Woessner, 1983), but sandy soils are also present (Fearnside and Rankin, 1979). The region is a mosaic of several vegetation types, especially broad-leaf equatorial forests, dense forests, sub-montane forests, high plateaus and high terraces (*terra fir*me forests), open broadleaf forests, savannas, alluvial fields and woodlands (Andrade *et al*., 2017). Primary forests within the forestry concession are subject to extractivism of non-timber forest products and low levels of subsistence hunting (Barlow *et al*., 2010; Parry *et al*., 2009).

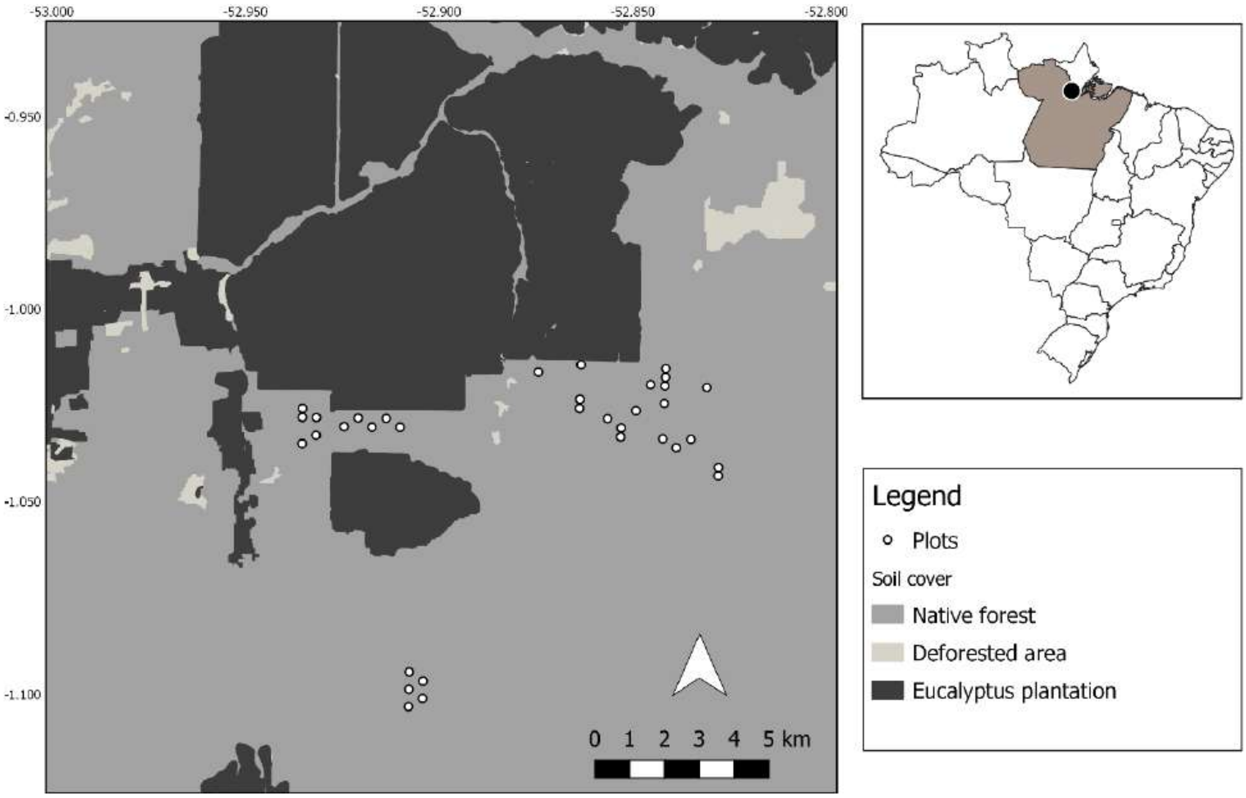

Fig. 1. Map of the study area: plots, deforested areas, native forests, and eucalyptus plantations.

2.2.2 Dung beetles sampling

Dung beetles were surveyed at 34 plots located within native undisturbed forests (Fig. 1), between June and July 2012. Each plot received a grid of six sampling points located 100 m distant from each other and 75 m away from the plot edge. Each sampling point had a pitfall trap, which consists of a 1-L plastic recipient buried at a ground level and containing 250 ml of saline solution (water, liquid detergent, and salt). A bait container with ~40g of human and pig dung (1:4 ratio, Marsh et al., 2013) was suspended above each pitfall to attract beetle. This is considered the most appropriate method to collect dung beetles (Favila and Halffter, 1997). A plastic cover protected both the pitfall and the bait container from rain. Beetles were collected after a 24-hour trap exposure in the field. All specimens were taken to the lab, where we sorted out and identified all dung beetles up to the lowest taxonomic level. To calculate the average biomass of each species, we obtained the dry weight of 15 individuals (when feasible) using a *Shimatzu AY220* 0.0001-g precision scale. The total community biomass was obtained by multiplying the average biomass of each species by its abundance. Collected material is deposited at the Scarabaeinae collection of Laboratório de Ecologia e Conservação de Invertebrados (LECIN) at the Federal University of Lavras, Brazil.

2.2.3 Data collection on environmental and landscape variables

To assess the influence of environmental variables on dung beetles, we measured the canopy opening, litter biomass, and soil texture in the same places in which pitfall traps were installed. To quantify the canopy opening, hemispheric photographs were taken with a Nikon FC-E8 fisheye lens attached to a Nikon D40 camera which was aligned at ca ~1.20 m above soil level. One picture was taken at each sampling point and six pictures were taken per plot. Aiming to standardize the harvesting and minimize mistakes, pictures were taken early in the morning and late in the afternoon or under a cloudy sky (Zhang *et al*., 2005). To estimate the canopy opening based on the pictures, the software Gap Light Analyzer (GLA version 2.0, Frazer *et al*., 1999) was used to calculate the ratio between the total amount of open space and the total area of the hemispherical photography (Frazer *et al*., 1999). This methodology is widely used to assess the canopy opening in tropical forests (Gries *et al*., 2012; Medjibe *et al*., 2014; Niemczyk *et al*., 2010; Silveira *et al*., 2010). Leaf litter was collected using a 25 x 25 cm square, placed randomly about 1m from each pitfall. We gathered one litter sample for each sampling point (six samples per plot). Samples were placed to dry in a 60°C greenhouse for 96 hours and, after that, dry weighed at a 0,001 g precision *Shimatzu AY220* (*Shimadzu Corporation*, Kyoto, Japan) scale. For the analysis, we used the average values of canopy openness and leaf litter biomass across the six sampling points per plot.

A soil sample (up to 10 cm deep) was collected in each sampling point. We mixed the six samples from each plot to represent the plot-level soil texture (clay, silt, and fractions of coarse sand). The amount of sand in the soil was considered as our measure of soil texture, as in previous studies (França *et al*., 2018; Gries *et al*., 2012; Griffiths *et al*., 2015). Granulometric analysis was conducted in the Jari Celulose S.A. soil lab. The distance to *Eucalyptus* plantations was estimated by using a GPS to georeference each sampling points, while information on planting areas was obtained through a shapefile provided by Jari Florestal. The smallest distance to sampling points as to the eucalyptus planting areas was measured using software Quantum Gis (version 3.4.15) and plugin NNJoin (https://plugins.qgis.org/plugins/NNJoin/) which joins two vector layers (the entrance layer and the merging layer) based on closer neighbor relations and closest distance up to the *Eucalyptus* planting edge.

2.2.4 Statistical analysis

Multicollinearity between predictor variables (canopy opening, litter biomass, percentage of sand and eucalyptus distance) was assessed with the variance inflation factor (VIF), using a *vif* function in *car* package (Fox and Weisberg, 2019), in software R (R Core Team, 2021). VIF value was smaller than 2.53 in all cases, indicating low multicollinearity. We, therefore, used the complete set of explanatory variables in all models (canopy opening, litter biomass, percentage of sand, and distance to eucalyptus). Spatial autocorrelation was tested separately for the species composition and biomass data using Mantel tests (Legendre and Legendre, 1998), with 1000 permutations using the *mantel* function in the *vegan* package (Oksanen *et al*., 2020).

To control the number of individuals' effects over the species richness observed, we also estimated the richness expected (rarefied richness) using *rarefy* function of the *vegan* package (Oksanen *et al*., 2020). Rarefaction is an approach used to establish the standardization of sampling efforts and thus, allow a straightforward comparison of results between groups showing differences in the abundance patterns (Barlow *et al*., 2007). Linear models with Gaussian distribution were used for continuous dependent variables (rarefied richness and biomass). For species richness and abundance variables, we used General Linear Models (GLM) with Poisson distribution and the “overdispersion” was corrected using Quasipoisson adjustment whenever necessary.

The effect of environmental variables on the composition of the dung beetles assemblage was also assessed. First, spatial autocorrelation was tested in our composition data using Mantel tests, and then, the assemblage dimension was reduced through a Principal Coordinate Analysis (PCoA) using a Bray-Curtis and Jaccard distance for abundance and presence-absence data, respectively. Species with only one or two records were removed from the analysis. Then, two axes (PCoA1) were used in a multivariate multiple regression mode, using all explanatory variables listed above. The result was plotted using the Poncho function (Dambros, 2020), which classifies the species along the gradients identified in the previous analysis.

To assess the most important drivers of dung beetle assemblages, we used a hierarchical partition analysis (Chevan and Sutherland, 1991) to compare the relative and independent importance of our four predictor variables for rarefied richness, abundance, and total biomass of the dung beetle communities. 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. 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. The significance of independent effects for each explanatory variable was calculated by randomized tests with 1,000 permutations (Mac Nally et al., 2002; Mac Nally and Walsh, 2004).

2.3 Results

We collected 3,722 dung beetles distributed in 13 genera and 49 species (Table 1). The nine most abundant species corresponded to ~85% of the individuals collected. *Oxysternon festivum* was the species with the largest number of individuals (502), followed by *Eurysternus caribaeus* (489) and *Onthophagus haematopus* (422). On the other hand, *Sulcophanaeus faunus, Oxysternon durantoni, Dichotomius worontzowi, Dichotomius latilobatus, Dichotomius* sp. 1, and *Ateuchus* sp. B presented only one individual each. A weak spatial autocorrelation was identified for dung beetle species composition and biomass (r = 0.46 and 0.24, respectively; p = 0.001).

Table 1. Species and number of individuals (N) collected in pitfalls in undisturbed forest area under the influence of eucalyptus plantations in the Jari region, Pará state, Brazilian Amazon.

Species	N	**Species**	N
Oxysternon festivum	502	*Eurysternus hamaticollis*	9
Eurysternus caribaeus	489	*Canthidium* sp. *K*	8
Onthophagus haematopus	422	*Onthophagus bidentatus*	8
Eurysternus caribaeus	356	*Eurysternus balachowskyi*	7
Dichotomius lucasi	348	*Ateuchus* sp. *D*	6
Deltochilum aff. submetallicum	327	*Ateuchus* sp. *E*	6
Ateuchus aff. murray	284	*Canthidium aff. lentum*	5
Canthon triangularis	278	*Deltochilum orbiculare*	5
Deltochilum septemstriatum	136	*Dichotomius subuaneus*	5
Canthidium sp. *B*	69	*Onthophagus onthochromus*	5
Dichotomius boreus	56	*Trichillum pauliani*	5
Canthidium aff. deyrollei	50	*Dichotomius imitator*	4
Ontherus carinifrons	46	*Canthidium* sp. *G*	3
Ateuchus pauki	38	*Canthon quadrigutatus*	3
Deltochilum sp. *B*	37	*Canthidium* sp. *I*	2
Eurysternus foedus	34	*Coprophanaeus dardanus*	2
Uroxys sp. *C*	30	*Coprophanaeus jasius*	2
Eurysternus ventricosus	27	*Eurysternus howdeni*	2
Canthidium sp. *D*	21	*Ateuchus* sp. *B*	1
Coprophanaeus lancifer	19	*Dichotomius latilobatus*	1
Ateuchus sp. *A*	15	*Dichotomius* sp. *1*	1
Deltochilum icarus	14	*Dichotomius worontzowi*	1
Ateuchus aff. connexus	13	*Oxysternon durantoni*	1
Ateuchus sp. *F*	9	*Sulcophanaeus faunus*	1
Canthidium sp. *M*	9		

Litter biomass varied from 18.1 to 50.7 g (30.4 ± 9.11 g), canopy opening varied from 8.5 to 15.42% (11.5 ± 1.72%), soil sand percentage varied from 62.6 to 95.2% (79.9 ± 10.98%), and the closest distance up to the edge of eucalyptus plantations varied from 178 to 4,226 m (1,739 ± 1,315 m).

2.3.1 Species richness, abundance, and biomass

Dung beetle species richness varied from 9 to 26 (M_e = 16.6 ± DP = 4.5) per plot. At each 1,000 m of distance to *Eucalyptus* plantation, species richness reduced by 10% (*coef* = -0.0001, *t*= -2.32, p = 0.027, Poisson GLM; Fig. 2). Rarefied species richness varied from 8.1 to 16 (M_e =11.3 ± DP = 1.74) per plot and was negatively influenced by canopy opening (β = -0.38, *t* = -2.26, *p* = 0.03, r^2 = 0.15; Fig. 3a) and by soil sand percentage (β = -0.09, *t* = -2.54, *p* = 0.01, r^2 = 0.18; Fig. 3b).

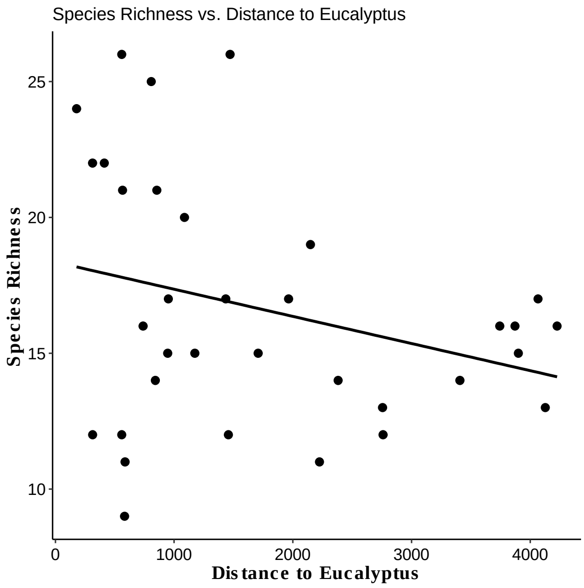

Fig. 2. Effect of proximity to *Eucalyptus* plantations on the species richness of dung beetles within undisturbed primary Amazonian forests, Pará state, Brazil.

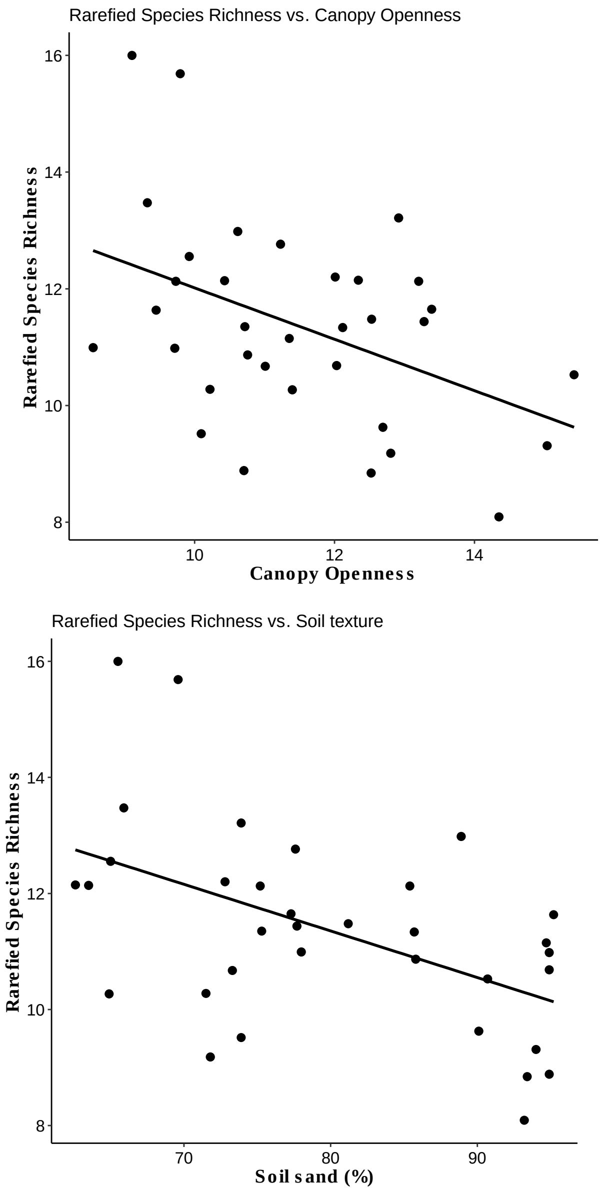

Fig. 3. Rarefied species richness of dung beetles in relation to canopy openness (a) and soil sand percentage (b) in undisturbed primary Amazonian forests under the influence of *Eucalyptus* plantations, Pará state, Brazil.

Dung beetle abundance varied from 38 to 356 individuals (M_e = 109.5 ± DP = 63.5) per plot. At each 1,000 m distant from the *Eucalyptus* plantation, abundance declined by 28% (*coef* = -0.0002, *t*= -3.1, p = 0.004, Poisson GLM; Fig. 4). Dung beetle biomass varied from 2.15 to 11.45 grams (M_e = 5.79 ± DP = 2.6 grams) per plot, but did not respond significantly to any explanatory variables (*p* > 0.05, data not shown).

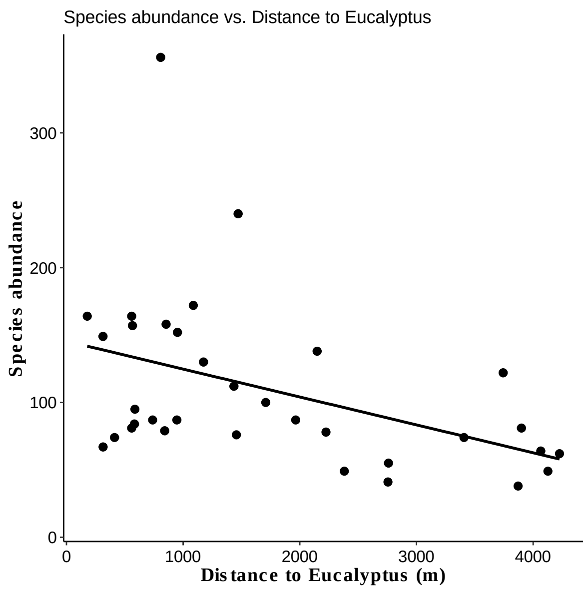

Fig. 4. Effect of distance to *Eucalyptus* on the number of dung beetles individuals collected in undisturbed primary Amazonian forests, Pará state, Brazil.

2.3.2 Species structure and composition

The first two axes of PcoA explained 32% of the variation in the dung beetle assemblage structure (Table 2). The percentage of sand in the soil (Fig. 5) and the distance to *Eucalyptus* (Fig. 6) significantly influenced the assemblage structure, both to the first and to the second axis of PcoA (results confirmed by MANOVA; Table 2). *Ontherus carinifrons, Canthidium aff. deyrolley,* and *Canthidium* sp. G were the most predominant in sandier soils, while *Onthophagus bidentatus, Canthon triangularis* and *Ateuchus* sp*. D* occurred mainly in less sandy soils. *Ateucus* sp*.* B and *Trichillum pauliani* occurred mainly within a longer distance to the eucalyptus plantation, while *Canthidium aff. deyrolley, Deltochilum* sp*. B* were observed only in areas close to eucalyptus plantations. The first two axes of PcoA explain 30.4% of the variation in the composition of species, which was significantly influenced by the percentage of sand in the soil, by the percentage of canopy opening, and by the distance to *Eucalyptus* (Table 2; Fig. 7).

Table 2. Results of multivariate multiple regression on the effects of environmental and landscape variables on the structure (relative abundance) and composition of dung beetles species (presence-absence). The values outside the parenthesis indicate the regression coefficients. Significant p-values are in bold.

	Variance explained	% of sand	Litter	Canopy cover (%)	Distance to Eucalyptus	R^2-adj
Bray-Curtis						
PCoA 1	17	0.009 (**0.02**)	-0.001 (0.75)	0.008 (0.68)	0.000 (**0.002**)	0.27
PCoA 2	15	-0.01 (**0.000**)	-0.001 (0.55)	0.003 (0.74)	0.000 (**0.01**)	0.78
Pillai-Trace		**(0.000)**	(0.836)	(0.901)	**(0.003)**	
Jaccard						
PCoA 1	20.8	0.013 (**0.001**)	-0.001 (0.72)	0.017 (0.34)	-0.000 (0.92)	0.46
PCoA 2	9.6	-0.002 (0.40)	0.008 **(0.04)**	-0.039 **(0.01)**	-0.000 (**0.01**)	0.20
Pillai-Trace		**(0.007)**	(0.122)	**(0.038)**	**(0.047)**	

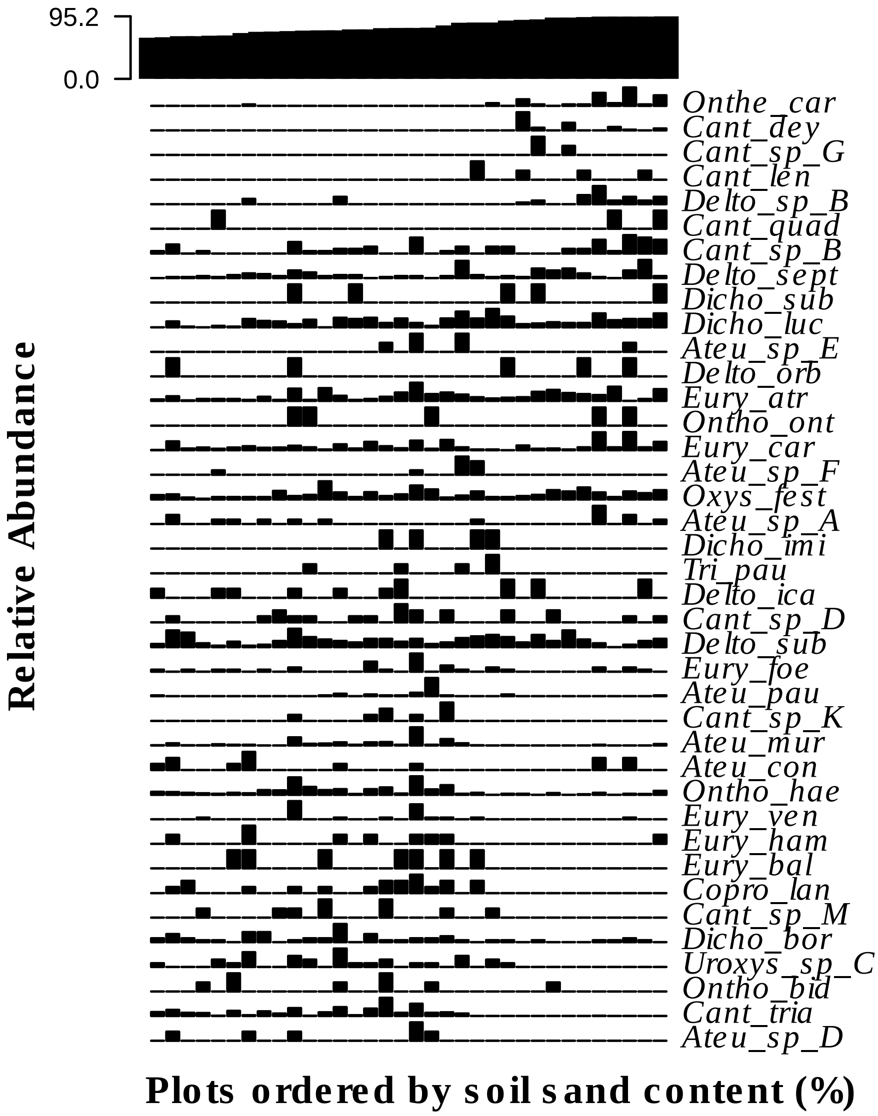

Fig. 5. Composition of dung beetles species due to the percentage of sand in the soil, collected in undisturbed primary Amazonian forests, Pará state, Brazil.

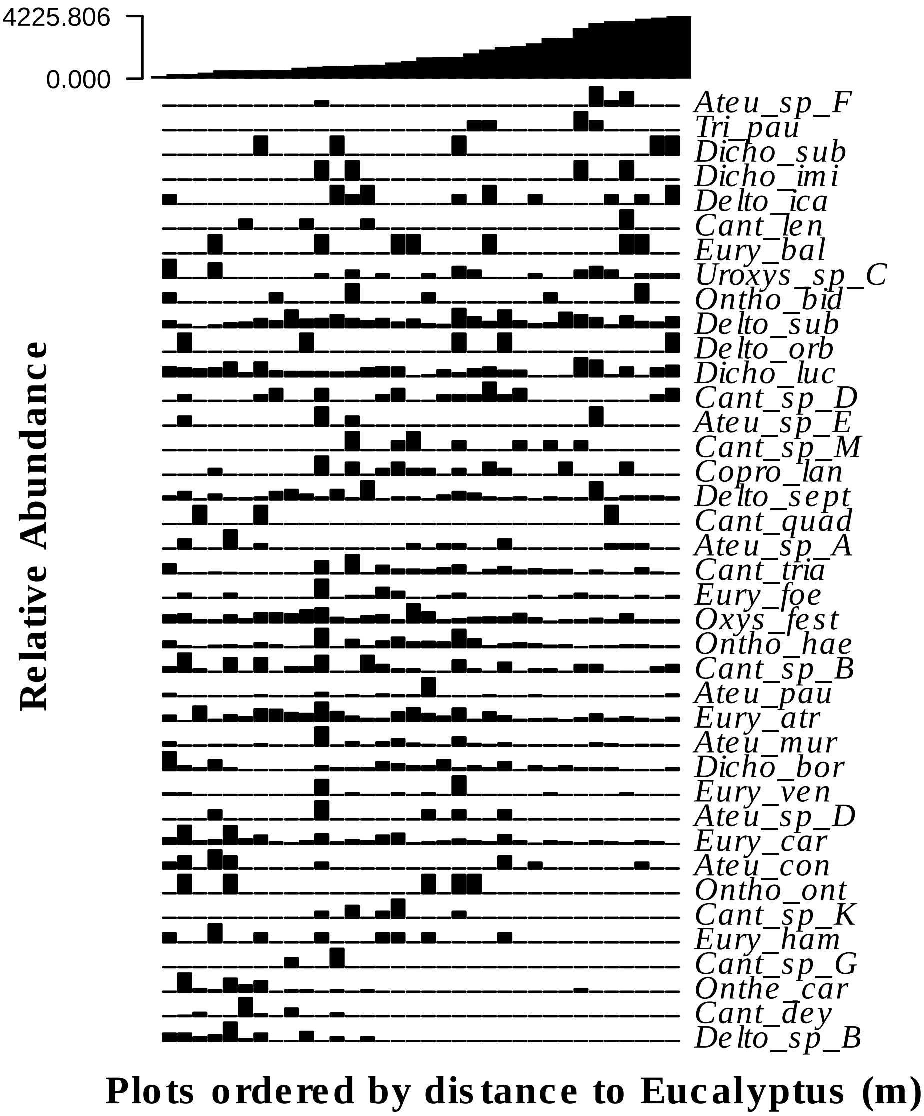

Fig. 6. Composition of dung-beetle species due to the distance of eucalyptus plantations, collected in undisturbed primary Amazonian forests, Pará state, Brazil.

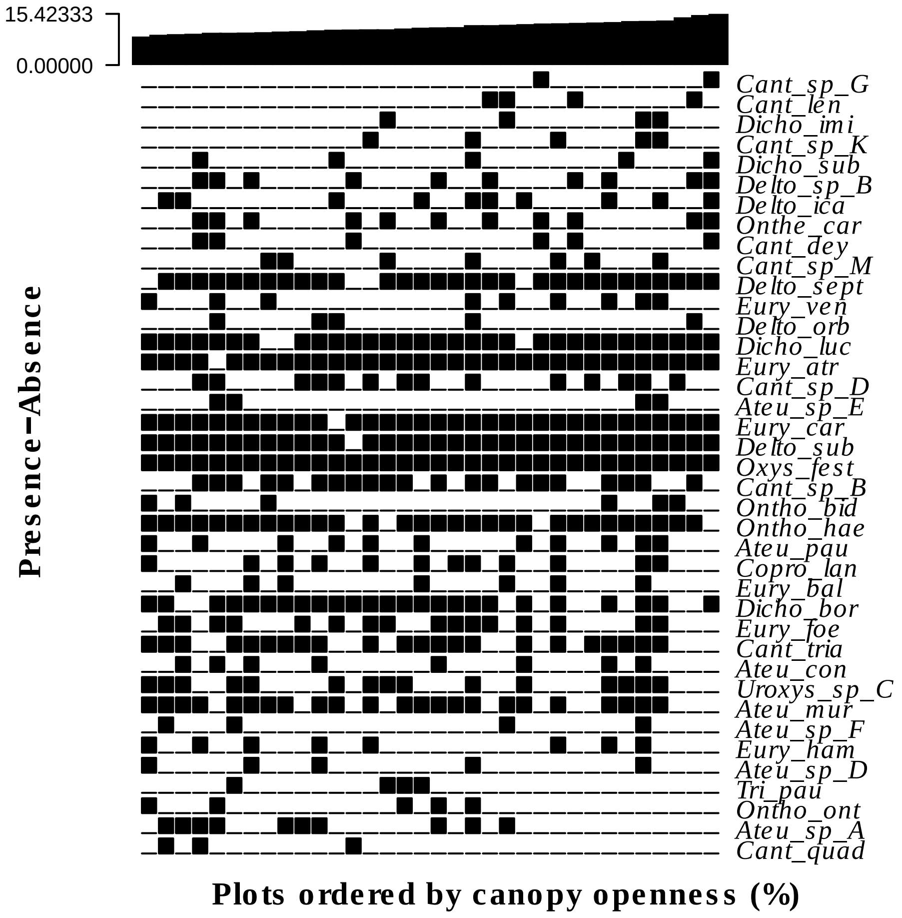

Fig. 7. Composition of dung beetles species (presence-absence data) due to the percentage of sand in the soil, collected in undisturbed primary Amazonian forests, Pará state, Brazil.

2.3.3 Relative importance of explanatory variables for dung beetles assemblages

Hierarchical partitioning and randomization tests reinforced GLM results showing the influence of environmental variables for the dung beetle assemblages (Fig. 8). Canopy opening and soil sand content have significantly influenced the rarefied species richness, while the distance to *Eucalyptus* explained significantly and in an independent way the changes in the total abundance and biomass of dung beetles assemblages.

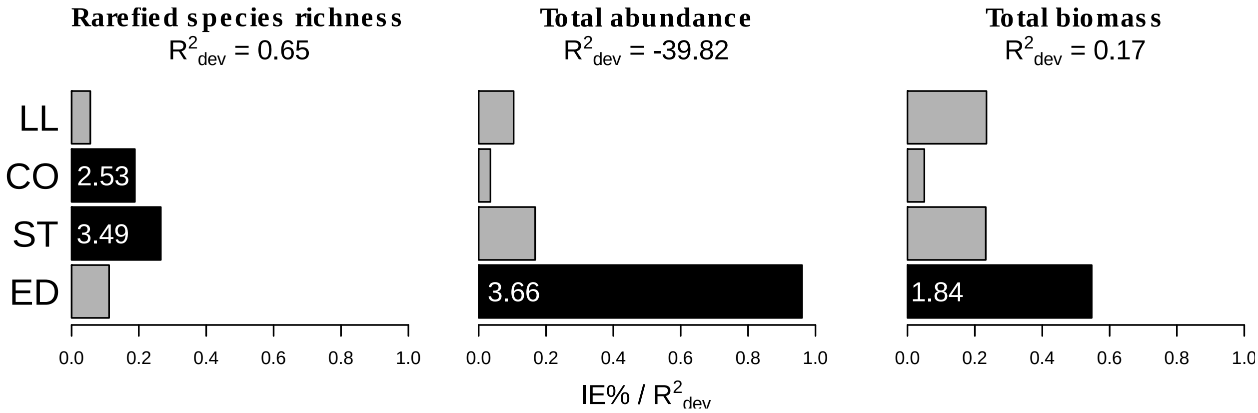

Fig. 8. Distribution of percentage of independent effects of different predictors of dung beetles assemblages in undisturbed primary Amazonian forests. The x-axis represents the percentage of independent effects (I%) divided by the total variance explained by the model (R^2_{de}). LL = litter weight (g), CO = canopy opening (%), ST = soil texture (% of sand) e ED = distance to eucalyptus (m). Black sticks represent significant effects (α = 0.05) established by randomized tests. Z values for the distribution produced by the 1,000 randomization of independent effects were calculated as indicators of the significance based on the 0.95 (Z ≥1.65) confidence interval.

2.4 Discussion

Although previous studies have compared biodiversity between planted forests and native forests (Beiroz *et al*., 2019; Gardner *et al*., 2008), we do not know studies that assess how forest monoculture plantations influence insects' fauna in nearby undisturbed forests in Amazonia or any other tropical regions. While addressing this knowledge gap, our results show the influence of proximity to *Eucalyptus* monoculture, canopy opening and soil texture on dung beetles communities from Amazonian forests. Understanding our results is important in the context of the development of exotic tree species initiatives, which has been spreading through the Amazon and other tropical forested regions over the last decades (Barlow *et al*., 2007; De Oliveira *et al*., 2019; Aguiar *et al*., 2014; Benami *et al*., 2018; Campos *et al*., 2021; Homma and Vieira, 2012; Stephens and Wagner, 2007).

The rarefied species richness of dung-beetle species declined with the increase of the canopy opening and the percentage of sand in the soil. In little less than 30% increase of sand percentage in the soil (62.6 – 95.2), on average there was a reduction of three species, about the same amounts of species lost with the increase of ~7% in the canopy opening. Dung beetles are sensitive to alterations in soil texture (Griffiths *et al*., 2015; Nichols *et al*., 2007; Silva *et al*., 2015) and to the canopy structure of the forest (Gómez-Cifuentes *et al*., 2019; Horgan, 2005). Salomão *et al*. (2022) have shown that the increase in the percentage of clay positively affects the number of tunneler beetle species, but not of roller or resident beetles. However, they have studied much less sandy soils (20.8±10.4%) than our study did (80±11%). Few species seem to tolerate very sandy soils, which retain less moisture and have a low compaction capacity, which results, respectively, in the desiccation of food resources and makes it more difficult to build nesting tunnels (Lumaret *et al*., 1991; Sowig, 1995).

In our area of study, only four species (*Ontherus carinifrons, Canthidium aff. deyrolley, Canthidium* sp*., and Canthidium aff. lentum*) seem to tolerate extremely sandy soils, since these species were only recorded in areas with more than 70% of the amount of sand. Sandy soils may become even more desiccated in larger canopy openings, since these openings are responsible for regulating the microclimate conditions of the soil and the understory, such as temperature, dampness, and radiant heat in the environment (Davis *et al*., 2001; Tuff *et al*., 2016). Perhaps because of this, a subtle increase in canopy opening may have significantly and negatively affected the species richness of beetle in our study, a similar pattern to that found in several studies (da Silva, 2011; Gardner *et al*., 2008; Marinoni and Ganho, 2006; Navarrete and Halffter, 2008; Nichols *et al*., 2007; Qie *et al*., 2011; Viegas *et al*., 2014)

Despite the effects on species richness, the distance to *Eucalyptus* plantations alone, but not soil texture and canopy opening, have significantly affected the abundance of individuals. By analyzing each functional guild separately, the distance to eucalyptus plantations was the only variable that influenced tunnelers and resident beetles, but not roller ones (data not shown). Beiroz *et al*. (2017) have shown a strong effect of soil on the total abundance of dung beetles in forests in the same region. This difference, however, may be a result of the spatial scale of the soil sample in that study (*ca.* 27 km on average) compared to ours (1.7±1.07 km). The relative effects of the distance to eucalyptus plantations on the abundance of dung beetles were demonstrated both by GLM and by the analysis of the hierarchical partition of variance. This demonstrates that reforestation of exotic species may influence biodiversity in surrounding native forests, thus promoting an increase of opportunistic species. This is worrisome if we consider that the new Brazilian Forest Legislation allows that the reclamation of 50% of legal reserves total areas in rural properties be made with exotic species (Brasil, 2012). Besides the risks related to invasion of exotic plant species (Zenni and Ziller, 2011), our study shows that there was not enough time for dung beetle assemblages to restructure after the impact, even decades after the eucalyptus plantation was concluded.

When we analyze the independent effects of each variable, our results demonstrate that the distance of eucalyptus planting was the only variable related to the abundance and total biomass of beetle communities (Fig. 8). The effects of *Eucalyptus* planting or other forest monocultures on dung beetles may occur directly or indirectly. For example, the proximity of exotic forest monocultures may reduce soil moisture due to high hydric demand (Poor and Fries, 1985) and also because the canopy allows the entrance of more light and heat, thus jeopardizing nesting of species most sensible to microclimate alterations (Nichols *et al*., 2007). It is also possible that the vertebrates' fauna is altered in the vicinities of the *Eucalyptus* plantation (Pattanavibool and Dearden, 2002; Terborgh *et al*., 2001; Umapathy and Kumar, 2000), thus reducing the availability of resources for dung beetles. In Brazil, forested planted with *Eucalyptus* may have a large diversity of mammal species (Piña *et al*, 2019), however, due to a uniform and scattered canopy, they cannot host large populations and diversity of large size primates (Gardner *et al*., 2008), which is one of the groups that most produced faces used by dung beetles as a food resource in Neotropic forests (Estrada *et al*., 1993; Feer, 1999).

Lastly, our study corroborates previous studies demonstrating the influence of forest degradation on tropical biodiversity (Barlow *et al*., 2016; França *et al*., 2018). Our results have shown, in particular, the importance of conservation strategies to mitigate the edge effects that exotic forest monocultures may cause in the biodiversity of nearby native forests.

CrediT authorship contribution statement

Maria Katiane S. Costa: Writing - original draft, Writing - review & editing. **Filipe M. França:** Supervision, Conceptualization, Methodology, Investigation, Resources, Data Curation, Formal analysis, Writing - review & editing, Project administration. **Carlos R. Brocardo:** Writing - review & editing, Formal analysis. **Rodrigo F. Fadini:** Supervision, Conceptualization, Formal analysis, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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