




Species diet and the effect of different spatial bait distribution on assemblage of dung beetles in Amazonian white-sand forest

Renato Portela Salomão^{1,2} · César Murilo de Albuquerque Correa³  · Sérgio Santorelli Junior⁴ · Albertina Pimentel Lima¹ · Wiliam Ernest Magnusson¹ · Eliene Fontes Arruda¹ · Ana Paula Vieira de Oliveira¹ · Ricardo Cesar Correa Cabral¹

Received: 3 November 2022 / Accepted: 24 April 2023
© African Association of Insect Scientists 2023

Abstract

The recognition and use of food resources in animal species may vary according to availability. Trophic niche and resource availability are among the most important drivers involved in the coexistence of species, which may require specific resources or exploit a large variety of resources. Dung beetle species feed from a wide range of food resources, including feces, carrion, and rotten fruit. The aim of this study was to assess the attractiveness and preference of different food types (dung, carrion, and banana) for dung beetles from a region of Amazonian white-sand vegetation (Campinarana). Closely spaced sets of pitfall traps (5 m of distance between traps) baited with different food types were installed to test food preference, and widely-spaced traps (150 m of distance) baited with different food types to test food-type attractivity. Overall, we captured 76 dung beetles of nine species, where *Deltochilum septemstriatum* Paulian (1938), was classified as a specialist of carrion, *Sylvicanthon proseni* (Martínez, 1949) and *Canthidium* gr. *lentum* were considered specialists of human feces, no species was considered generalist. In terms of assemblage parameters, although food type did not affect species richness or individual abundance in both trap-spacing approaches, the species composition of beetles collected in carrion-baited traps was distinct from that in feces-baited traps. Seven out of nine species were attracted towards one of the resource types, regardless of the trap spacing design. Therefore, we conclude that diet of dung beetles that dwells in Campinaranas are relatively strict, with species being attracted mostly to carrion or feces, regardless of the availability of other food types.

Keywords Diet · Insect Sampling · Niche breadth · Scarabaeinae

Introduction

The food choice highlights as a determinant feature among animals since it may affect individual condition and fitness (Agetsuma 1996; Massei et al. 1996; Nosil 2002; Servín-Pastor et al. 2021). Choice, recognition, and use of different

food types by animals may vary according to food availability in time and space (Agetsuma 1996; Massei et al. 1996). Also, species traits, such as mobility, and habitat distribution may determine the individual food preferences and foraging strategies (Sailer et al. 1985; Curtis et al. 2015; Bourg et al. 2016). Although diets may include a broad range of food items, food choice reflects how individuals perceive and select food resources in their ecosystems (Agetsuma 1996; Bourg et al. 2016; Salomão et al. 2022a). Therefore, it is necessary to understand species food-choice patterns in relation to resource availability to determine how species trophic relationships are spatially structured.

Trophic niche breadth and resource availability are among the most important ecological factors involved in the coexistence of species in highly diverse ecosystems (e.g. tropical and subtropical forests) (Brown 1984; Gaston et al. 1997). Species show different degrees of specialization, some of which requiring specific resources (specialists or species

✉ César Murilo de Albuquerque Correa
correa.agro7@gmail.com

¹ Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas 69080-971, Brazil

² Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Mexico

³ Laboratório de Bioecologia de Scarabaeoidea (Scarabab), Universidade Estadual de Mato Grosso do Sul, Mato Grosso do Sul, Aquidauana 79200-000, Brazil

⁴ Instituto de Educação, Agricultura e Ambiente, Universidade Federal do Amazonas, Humaitá, Amazonas, Brazil

with low trophic-niche breadth) and others exploiting a large variety of resources (generalists or species with large trophic-niche breadth) (Krebs and Davies 1981; Sexton et al. 2017). Since generalists use several food resources they have a higher probability of meeting their resource needs in a larger number of habitats than do specialists (Swihart et al. 2003; Giménez Gómez et al. 2018). In addition, a broader trophic niche guarantees a constant input of energy for the basic biological processes (*e.g.* reproductive events), and consequently has a positive impact on the population dynamics and dispersal of species (Krebs and Davies 1981; Paine et al. 1981; Halffter and Halffter 2009). Among butterflies, for example, species with narrow niche breadth and with low resource availability show lower mobility than species with wider niche breadth and high resource availability (Komonen et al. 2004). Thus, trophic-niche breadth may expand the spatial population distribution in the case of generalist species or limit the colonization of new habitats when species are specialists (González-Solís et al. 1997; Sexton et al. 2017).

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) constitute an important decomposer group, feeding mostly from decaying material (Halffter and Mathews 1966; Halffter and Halffter 2009; Scholtz et al. 2009). Besides coprophagy, species feed on other food types, such as carrion, rotten fruits, flowers, live arthropods, and fungi (Larsen et al. 2006; Noriega and Calle 2008; Halffter and Halffter 2009; Correa et al. 2023). There is a wide variation in species diet breadth among dung-beetle species, with species that feed only from one resource type (*e.g.* strictly coprophagous) to those that feed on many types of food (Schmidt et al. 2004; Larsen et al. 2006; Noriega 2015; Frank et al. 2018; Giménez-Gómez et al. 2018). However, some authors suggest that most dung beetles are food generalists (Scholtz et al. 2009; Frank et al. 2018; Raine and Slade 2019), and will feed from different resources depending on their spatial availability.

In order to understand if beetles use a resource depending on its availability or if beetles are specialized on one food resource type, field studies have frequently used pit-fall-baited traps to test resource attractiveness for the dung beetle species (Bourg et al. 2016; Salomão et al. 2017). However, most studies test species diet by offering spatially close food resources (*i.e.* from 2 to 30 m, see Filgueiras et al. 2009; Noriega 2012; Correa et al. 2016; Ferreira et al. 2020). Regarding the dung beetles' diet, attraction to food may comprise a broad range of interactions, encompassing the recognition and use of a food resource (*e.g.* mediated by olfactory positive responses) (Larsen et al. 2006; Salomão et al. 2017). Food preference (*i.e.* food choice) involves the election of specific food types among different available options (Stavert et al. 2014; Salomão et al. 2017). Therefore, to test attractiveness of different food resources, it is necessary to offer them simultaneously (hereafter 'food

preference') and isolated (hereafter 'food attractiveness') from each other so that scale-specific attractiveness and preference can be distinguished.

The aim of this study was to assess the food resource attractiveness and preferences in the dung beetle assemblage, and from each species, from a region of Amazonian white-sand vegetation. We tested three resource types (bovine carrion, human feces, and rotting banana). We offered each resource type isolated from the others as a proxy of resource attractiveness, and we offered the three resources simultaneously to test resource preference. To assess the effects of resource type on dung beetle diversity, we analyzed their data at assemblage scale (species richness, abundance, assemblage structure) and species scale, which are the common assessments to understand trophic dynamics in dung beetles (*e.g.* Filgueiras et al. 2009; Bourg et al. 2016; Salomão et al. 2017). Depending on the availability of food resources in the environments, animals may recognize them differently (Lemke 1984; Alm et al. 2002). Among dung beetles, their food comprises a scarce, ephemeral and unpredictably distributed resource (Hanski 1990; Hanski and Cambefort 1991; Scholtz et al. 2009). Besides, dung beetles may adapt their food use depending on the individual condition (*e.g.* reproductive moment) and environmental conditions, as land-use change and food resource scarcity (Hanski and Cambefort 1991; Halffter and Halffter 2009; Bourg et al. 2016; Tocco et al. 2021). Therefore, we expected that each resource type will record different species richness, and assemblage structure, which will depend on the spatial distribution of the resources. Moreover, as dung beetle species are mainly coprophagous (Hanski and Cambefort 1991; Larsen et al. 2006; Scholtz et al. 2009), we expected that most species will be categorized as coprophagous.

Material and methods

Study area

This study was carried out in the Rio Negro Sustainable Development Reserve (RDS Rio Negro, 3°01'S; 60°48'W, 70 m a.s.l.). The reserve is located in the municipalities of Manacapuru, Iranduba and Novo Airão, state of Amazonas, Brazil. The vegetation that predominates in the study area is the white-sand Campinarana, opener sandy heath (Campina) and dense rainforest. We carried out the study in Campinarana vegetation, a sandy tropical forest that has high groundwater levels (Junk et al. 2011). The climate is classified as Af according to Köppen's classification, with an average annual temperature of 26.4 °C and with a mean annual precipitation of 3,345 mm (Climate-Data 2021). The dry season usually occurs between June and November (mean monthly rainfall: 172 mm), and the wet season

from December to May (mean monthly rainfall: 385 mm) (Climate-Data 2021).

Data collection

We performed two trap-spacing approaches, in October 2021, to test the attractiveness and preference of different food resources for dung beetles. For this, sampling units (*i.e.* set of pitfall traps) were intercalated throughout the study area (sampling units of the trap-spacing approach 1 and 2 were spatially intercalated). The two trap-spacing approaches were set up at the same time. For both approaches, we used fresh human feces, rotting bovine carrion (*i.e.* beef), and rotting banana, which are commonly used as baits for dung beetles in tropical American ecosystems (*e.g.* Horgan 2008; Filgueiras et al. 2011; Medina and Lopes 2014; Correa et al. 2016).

Trap-spacing approach 1: In order to test the attractiveness of each resource type, independent of the other baits used in this study, we installed five sets of pitfall traps. Each set comprised three traps, and each trap was baited with one food resource type (one trap baited with human feces, one with carrion, and one with banana). In each set, traps were spaced 150 m from each other to avoid attractive effects of each resource type (da Silva and Hernández 2015). Each set of traps spaced 300 m apart.

Trap-spacing approach 2: To test food preference, we installed six sets of pitfall traps, each set comprised of three pitfall traps (each one with a different resource type) spaced 5 m from each other in a triangular shape, thus allowing the beetles to choose among resources. Each set was spaced 600 m apart.

Considering the flight activity and spatial dispersion of dung beetles (Hanski and Cambefort 1991; Larsen and Forsyth 2005; Silva and Hernández 2015), food resources that are spaced 150 m among each other would allow us to test food resource attractiveness *per se* (*i.e.* food attractiveness experiment), but not the food choice itself. Following this rationale, by offering food resources that are spaced 5 m among each other, we could detect dung beetles' food choice (*i.e.* food preference). The dung beetles that fell in pitfall traps of trap-spacing approach 2 in theory would prefer among other spatially close options. The distance of food preference in the current study was used following similar studies of dung beetle diet (Filgueiras et al. 2009; Salomão et al. 2022a).

Pitfall traps consisted of a plastic recipient (100 mL) buried at soil and filled with ca. 250 mL of a killing solution (water, ca. 5 g of salt, and ca. 5 g of detergent), to capture and preserve specimens. A 50 mL plastic cup with ca. 20 g one of the attractive baits (see the following paragraph) was set above this recipient. To decompose bovine carrion and banana, we kept them in separate plastic bags for 24 h before installing the traps. Since this project is a final product of

a postgraduation field course, we had logistical limitations regarding the period used for carrion and fruit decomposing, as well as to keep traps installed in field. A 48-h period is commonly used for rotting carrion and fruits in dung beetle studies (*e.g.* Iannuzzi et al. 2016); however, there are studies that successfully assess dung beetle assemblages by using fresh meat (*e.g.* Favila 2005). To avoid the entrance of rain-water and twigs, a plastic lid was attached on the top of the trap. The baited pitfall traps were left for 24h. Although pitfall traps commonly are kept in field during 48 h (Liberal et al. 2011; Medina and Lopes 2014), 24 h is an adequate period to keep pitfall traps in the field in order to properly sample dung beetle assemblages in the tropics (Barraza 2010; Braga et al. 2013). After 24 h, the dung beetles were collected and stored in vials with ethanol 70%.

Dung beetle species were identified using identification keys (Génier 2009; Vaz-de-Mello et al. 2011; González-Alvarado and Vaz-de-Melo 2021), and by comparison with authoritatively identified specimens deposited in the entomological collection of the Instituto Nacional de Pesquisas da Amazônia (INPA; Manaus, Amazonas, Brazil). Specimens were deposited in the entomological collection of INPA.

Data analysis

Since data obtained from pitfall traps baited with rotten banana captured only one dung beetle, we did not include this resource type in the statistical analyses.

To evaluate the effect of food preference and food attractiveness at assemblage scale (on dung beetle species richness and abundance), we used separated generalized linear models (GLMs). For each trap-spacing approach, food type (*i.e.* bovine carrion and human feces) was used as the predictor variable, and dung beetle species richness or abundance was used as the response variable. We used Poisson error distribution for both models. We analyzed the homoscedasticity assumption with Fligner–Killeen tests, evaluating the distribution of data by using Q-Q plots. We tested the presence of outliers with Cook's distance. Statistical analyses followed Zuur et al. (2009) and Crawley (2013) and were conducted in R software version 3.2.3 (R Core Team 2015).

To illustrate the differences in dung-beetle assemblages collected in carrion and human feces from both food preference and food attractiveness approaches, we used non-metric multidimensional scaling (NMDS) with 2,500 permutations. We considered four treatments (food preference and attractiveness of carrion and feces). To assess assemblage dissimilarities, we used the Bray-Curtis index. To test for statistical differences among the four treatments, we used permutational multivariate analysis of variance (PERMANOVA) with 9999 permutations. To evaluate the multivariate dispersion of the data in each treatment, we used permutational multivariate

analysis of dispersion (PERMDISP) and 999 permutations (Anderson 2006). The NMDS was undertaken in Primer software (Clarke and Gorley 2006), and the PERMANOVA and PERMDISP were conducted with vegan and lattice packages, respectively (Oksanen et al. 2020; Sarkar 2021), in R software (R Core Team 2015).

To classify dung beetle species as food specialist or food generalist, we used multinomial classification (CLAM) approach (Chazdon et al. 2011). To calculate CLAM, we used a specialization threshold of $K = 0.667$ and $P = 0.05$ (Bicknell et al. 2014). Thus, species were categorized as coprophagous, necrophagous or diet-generalist. This analysis was performed with the vegan package in R (R Core Team 2015; Oksanen et al. 2020).

Results

We collected 76 dung beetles from nine species and seven genera (Table 1). *Deltochilum septemstriatum* Paulian (1938), *Canthidium* gr. *lentum* and *Sylvicanthon proseni* (Martínez 1949) were the dominant species, encompassing 69.73% of the dung beetles sampled. Three species, namely, *Ateuchus globulus* (Boucomont 1928), *Canthidium deyrollei* Harold, 1867 and *Ontherus carinicollis* Luederwaldt (1930), were each represented by only two individuals. In total, bovine carrion attracted 32 individuals of three species (*A. globulus*, *Deltochilum* gr. *guyanense*, *D. septemstriatum*), human feces attracted 43 individuals of eight out of nine species captured in the study (only *D. septemstriatum* was not recorded in human feces) (Fig. 1). Considering total data, six species were exclusively recorded in human feces, two species (*A. globulus* and *D. guyanense*) co-occurred in at least two of the three resource types, and *D. septemstriatum* was recorded exclusively in carrion.

In food preference approach, feces-baited traps recorded the highest species richness and abundance ($s = 8$, $n = 27$), followed by carrion ($s = 3$, $n = 18$), banana was the bait-type that recorded least species and abundance ($s = 1$, $n = 1$). In addition, in food preference approach, six of the eight species recorded in human feces were exclusively captured in this bait type (Table 1). In food attractiveness approach, five species and 16 individuals were captured in feces-baited traps, two species and 14 individuals were captured in carrion-baited traps, and no dung beetles were collected in banana-baited traps. In this approach, each species were attracted to a specific resource type. In both food attractiveness and food preference approach, there were no statistical difference in dung beetle species richness recorded in feces and carrion (food attractiveness – $X^2_{1,5} = 2.564$, $P = 0.499$; food preference – $X^2_{1,9} = 5.466$, $P = 0.283$) or abundance (food attractiveness – $X^2_{1,5} = 9.426$, $P = 0.674$; food preference – $F_{1,9} = 10.719$, $P = 0.277$).

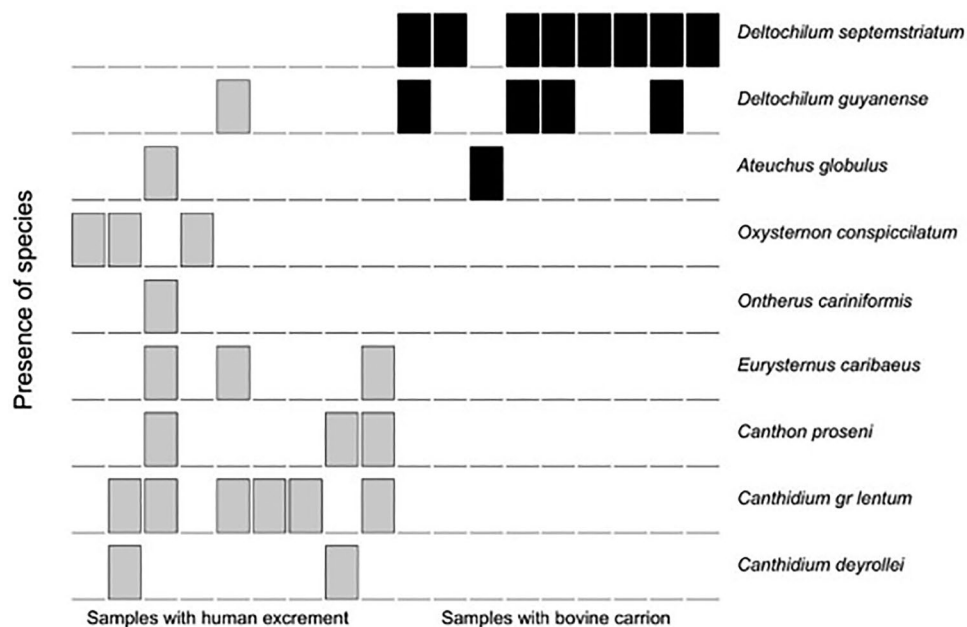
PERMANOVA indicated a statistical difference among assemblages recorded in each resource type ($F_{3,14} = 2.894$, $P = 0.002$). Species tended to be attracted towards one of the resource types (carrion vs. human feces), in both the food-attractiveness and food-preference trap-spacing approaches (Table 1; Fig. 2). For example, *D. septemstriatum* was recorded in both trap-spacing approaches, but exclusively in carrion-baited traps (Table 1). On the other hand, *Canthidium deyrollei*, *Canthidium* gr. *lentum*, *S. proseni*, *Eurysternus caribaeus* (Herbst, 1789), and *Oxysternon festivum* (Linnaeus, 1758) were also recorded in both approaches, but exclusively in feces-baited traps (Table 1).

Of the nine species collected, *D. septemstriatum* was classified as a specialist of carrion (necrophagous), *S. proseni* and *C. gr. lentum* were considered specialists of human feces (coprophagous), no one was classified as generalist, and for the six remaining species it was not possible to determine

Table 1 Dung beetles collected with bovine carrion, human feces, and rotten banana at food preference (FP) and attractiveness (AT) approaches in eleven sampling sites located in white-sand Amazon forests at RDS do Rio Negro, Amazonas, Brazil

| Tribe | Species | Resource removal strategy | Bovine carrion | | Human feces | | Rotten banana | | Total abundance |
|--------------|--|---------------------------|----------------|--|-------------|----|---------------|----|-----------------|
| | | | FP | AT | FP | AT | FP | AT | |
| | | | Ateuchini | <i>Ateuchus globulus</i> (Boucomont, 1928) | Tunneller | 1 | | 1 | |
| Dichotomiini | <i>Canthidium deyrollei</i> (Harold 1867) | Tunneller | | | 1 | 1 | | | 2 |
| | <i>Canthidium</i> gr. <i>lentum</i> | Tunneller | | | 8 | 6 | | | 14 |
| | <i>Ontherus carinicollis</i> (Luederwaldt 1930) | Tunneller | | | 2 | | | | 2 |
| Deltochilini | <i>Deltochilum</i> gr. <i>guyanense</i> | Roller | 3 | 1 | 2 | | 1 | | 7 |
| | <i>Deltochilum septemstriatum</i> (Paulian 1938) | Roller | 14 | 13 | | | | | 27 |
| | <i>Sylvicanthon proseni</i> (Martínez 1949) | Roller | | | 8 | 4 | | | 12 |
| Oniticellini | <i>Eurysternus caribaeus</i> (Herbst 1789) | Dweller | | | 4 | 3 | | | 7 |
| Phanaeini | <i>Oxysternon festivum</i> (Linnaeus 1758) | Tunneller | | | 1 | 2 | | | 3 |
| | Total abundance | | 18 | 14 | 27 | 16 | 1 | 0 | 76 |

Fig. 1 Presence and absence of dung beetle species recorded with human excrement and bovine carrion in the Rio Negro Sustainable Development Reserve, Amazonas, Brazil



their food preference due to the low number of individuals collected (Fig. 3).

Discussion

Diet and trophic niche are key factors regulating the dynamics of competition, species distribution, and coexistence in natural and anthropic environments. This is especially

important in dung beetles, due to their fierce interspecific food competition (Hanski and Koskela 1977; Chamorro-Florescano et al. 2011) together with the changes in the quantity and quality of food in the Anthropocene (Birnie-Gauvin et al. 2017). Our results provided data regarding the diet of dung beetles from the Amazonian rainforest. Dung beetle assemblage was composed by species with strict coprophagous and necrophagous habits, but no generalists' species were found. The dung beetle diversity from a region

Fig. 2 NMDS ordination of the dung beetle assemblages recorded in pitfall traps baited with feces and carrion in the food attractiveness and preference trap-spacing approach in the Rio Negro Sustainable Development Reserve, Amazonas, Brazil

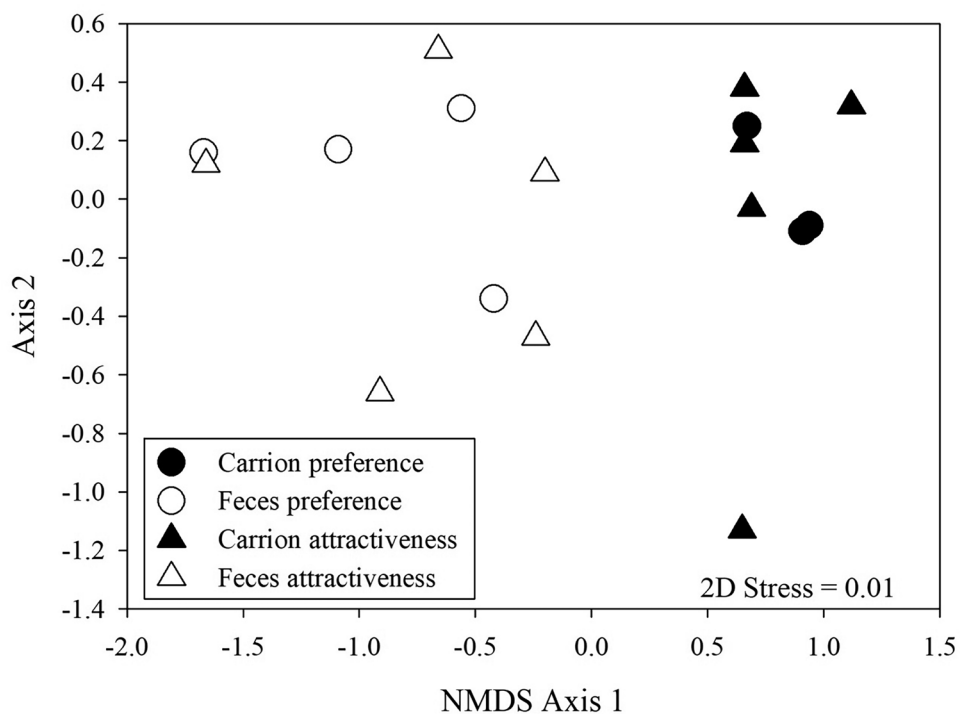
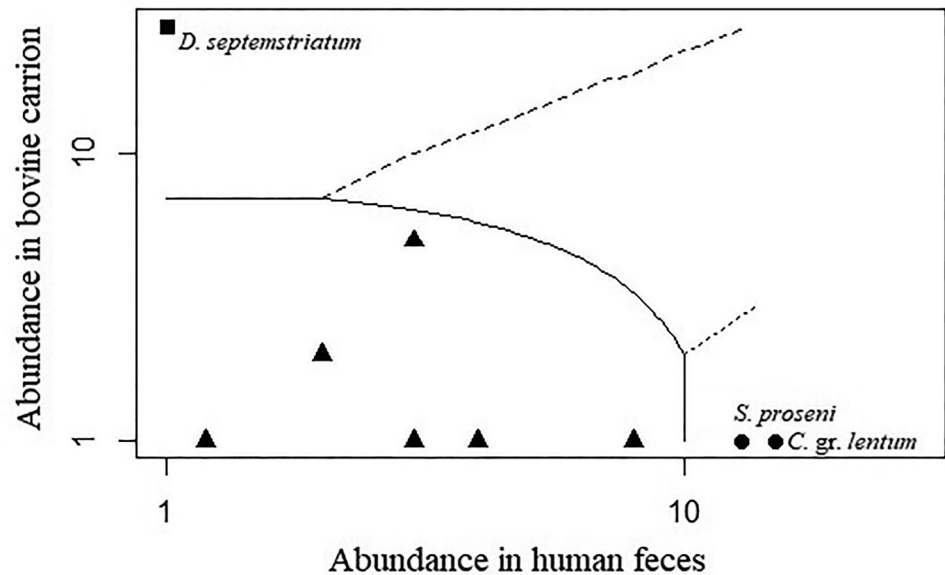


Fig. 3 Multinomial classification method for dung beetles sampled in pitfall traps baited with feces and carrion in the Rio Negro Sustainable Development Reserve, Amazonas, Brazil. Square = specialists of bovine carrion; Circle = specialist of human feces; and Triangle = rare. Dashed lines represent CLAM thresholds for specialist and generalist classes, and solid lines indicate the threshold at which species are too rare to classify



of white-sand forest showed similar trends of food attractiveness and food preference – a lack of difference of species richness and abundance between feces and carrion-baited traps, regardless of food availability.

We found that dung beetle assemblages attracted to human feces were distinct from those attracted to carrion. Indeed, of the nine species recorded, only two (*A. globulus* and *D. gr. Guyanense*) were collected on more than one resource type, one (*D. septemstriatum*) was collected exclusively on carrion, and the other six species were recorded exclusively in feces-baited pitfall traps. This occurred, in the first instance, because the dung beetles are able to select a specific food type using olfactory cues (Dormont et al. 2004, 2010; Stavert et al. 2014), causing a segregation of the dung beetle assemblage between food resources (e.g. carrion vs. feces). In other regions of Amazon forest, dung beetle assemblages comprise wider trophic niches when compared to our study (Ratcliffe 2013; Noriega 2015; Beiroz et al. 2018), which may suggest that white-sand forest present particular trophic dynamics in Amazonia. Nonetheless, it is important to consider that limiting environmental conditions (e.g. low soil productivity and vegetation complexity) in white-sand forests could result in strong environmental selection pressure (Borges 2004; Carvalho et al. 2021). Thus, the limiting environmental conditions imposed on dung beetles of white-sand forests may directly result in highly adapted fauna, which occupies narrow functional niches (e.g. trophic, microhabitat, period of activity).

In both food attractiveness and food preference trap-spacing approaches, there were no statistical differences in species richness and abundance of dung beetles recorded with human feces and carrion baits. This is an interesting result, considering that there are dung beetle species highly

attracted to carrion (e.g. *Canthon cyanellus* LeConte, 1859 and *Deltochilum verruciferum* Felsche (1911), see Bourg et al. 2016; Salomão and Iannuzzi 2017); however, in most cases feces is the food resource that attracts most individuals and species (Hanski and Cambefort 1991; Halffter and Halffter 2009). The difference in assemblage structure between bait types, but the absence of differences in species richness and abundance indicate that, although species captured in traps were distinct among bait types, the number of individuals captured were similar. In our study, we captured a relatively low number of individuals and species in each pitfall trap of our study, which ranged from one to fourteen specimens. It is important to consider that the study was conducted near the end of the dry season. Although dung beetle seasonality dynamics are unknown in Campiarana forests, some Amazonian regions have a strongly seasonal pattern of activity of dung beetle species (Correa et al. 2021, but see Ratcliffe 2013). Thus, our sampling could be biased due to the sampling period, but future studies should be conducted aiming to disentangle dung beetle seasonality patterns in Campinaranas.

Depending on food availability, insects may adapt their feeding behavior, using alternative resources (e.g. Halffter and Matthews 1966; Panizzi 2000; Boulay et al. 2005). Contrary to our expectations, some dung beetle species chose the same food independently of the availability of other ones. Indeed, in our study, we found one species considered necrophagous and two coprophagous species. According to dung beetle evolutive history, the Neotropical rainforests comprise species with contrasting trophic niche width (Hanski and Cambefort 1991; Scholtz et al. 2009), ranging from strictly coprophagous species (e.g. *Bradypodidium* spp. Vaz-de-Mello 2008, which apparently are

strictly related to sloth feces, Vaz-de-Mello 2008) to those that feed from a myriad of different food types (e.g. *D. veruciferum*, Salomão et al. 2017). Dung beetle that inhabits harsh environments can show specific strategies that range from flexible behavioral strategies (e.g. nesting plasticity) to physiological strategies aiming to surpass the limiting resource availability and climatic conditions (Rougon and Rougon 1991; González-Megías and Sánchez-Piñero 2004). The narrow relations between dung beetle species and food resource observed in our study may reflect the complex interspecific interactions dynamics in Campinarana ecosystem, but our analyses cannot distinguish between them. To assess dung beetle trophic niche breadth from a finer scale, different types of excrement or carrions could be used simultaneously, which has been barely considered in tropical ecosystems in South America (Filgueiras et al. 2009; Bogoni and Hernández 2014; Noriega 2015), especially in Amazon region (Frank et al. 2018).

To assess food choice depending on food availability, it is important to consider the spatial range in which species perceive their environment, as well as the food resources. As dung beetle daily movement in tropical ecosystems usually ranges from 50 to 250 m (Larsen and Forsyth 2005; da Silva and Hernández 2015), we believe that the distance among the traps in our food attractiveness trap-spacing approach was enough to avoid dung beetles from being able to choose a food resource. Such pattern of food preference, independent of the availability of other food types, has already been observed in dung beetle assemblages of Caatinga dry forest, a semi-arid ecosystem in South America (Salomão et al. 2017). In addition, previous dung preference experiments among primate species, as well as among different mammals, suggest that there are species with narrow niche preferences, being attracted just to one dung type (Ponce-Santizo et al. 2006; Filgueiras et al. 2009; Bogoni and Hernández 2014). Our results and these previous data may suggest that, although dung beetles from the Neotropical region present a wide range of diets, many species have a narrow niche breadth, presenting a behavior that we could consider non-opportunistic.

In the current study, we had a very small number of species and individuals when compared to other regions of Amazon ecosystem (see Ratcliffe 2013; Correa et al. 2021; Salomão et al. 2022b). It is important to consider our methodological limitations and the natural history of the studied ecosystem (Campinaranas). Our sampling effort was limited, both regarding the number of pitfall traps used and the number of samples, which are key elements to attain an adequate coverage of dung beetle species (Rivera and Favila 2022). In addition, the fact that we did not use sugarcane for banana decomposition and did not let it decompose for more than 24 h could have led to the low *n* of individuals in banana-baited traps (see Puker et al. 2021). Besides the

sampling issues, it is important to consider the dung beetle assemblage dynamics in Campinaranas. For example, sandy soils (which are predominant in Campinaranas) may affect dung beetle nesting activity and consequently its diversity (Fincher 1973; Silva et al. 2015). In Amazonian region, increases in the proportion of sand in soils of forested sites negatively affected the dung beetle diversity (Salomão et al. 2022b). Furthermore, in dry ecosystems from America and Africa dung beetle diversity is relatively low, which is related to the more challenging conditions that can filter specific species traits (Rougon and Rougon 1991; Liberal et al. 2011; Filgueiras et al. 2021; Sánchez-Bermejo et al. 2022). Although Campinaranas have a marked seasonal rainfall and flooding dynamic (Adeney et al. 2016), insect seasonality in the Campinaranas is still poorly known (Adis et al. 1989; Seixas et al. 2017). In order to present a broader and more complete comprehension of the dung beetles from this ecosystem, it is important to carefully study the other periods of the year. Nonetheless, this study allowed us to establish the first insights regarding dung beetle diet and trophic segregation in Campinaranas.

Conclusion

Our results demonstrate that diet of dung beetles that dwells in Campinaranas are relatively strict, with species being attracted mostly to carrion or feces, regardless of the availability of other food types. The natural history of an ecosystem plays a key role in determining strategies of animal species (Agetsuma 1996; Halffter and Halffter 2009; Nandintsetseg et al. 2019), which encompass their capacity to perceive and use food resources. Therefore, future studies should focus on understanding how the evolutive history of Campinaranas and the neighboring Amazon ecosystems determine feeding strategies that species present.

Acknowledgements RPS was supported by Programa Nacional de Pós-doutorado/Capes (Government funds PNPd/CAPES, Brazil) and by DGAPA post-doc fellowship from Universidad Nacional Autónoma de México. SSJ is supported by Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM/PROFIX – RH – Edital/009/2021).

Data availability The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

Declarations

Ethical approval The experimentation was no invasive and complied with Brazilian law. At the end of the study, the specimens were deposited in the Entomological Collection at the INPA (Manaus, Amazonas, Brazil) following standard procedures.

Human participants and informed consent There were no humans participants on the study and thus, no ‘informed consent’ was required.

Conflict of interest There are no conflicts of interest (financial and non-financial) among authors.

References

- Adeney JM, Christensen ML, Vicentini A, Cohn-Haft M (2016) White-sand ecosystems in Amazonia. *Biotropica* 48:7–23
- Adis J, Ribeiro EF, Morais JW, Cavalcante ETS (1989) Vertical distribution and abundance of arthropods from white sand soil of a Neotropical Campinarana forest during the dry season. *Stud Neotrop Fauna E* 24:201–211
- Agetsuma N (1996) Dietary Selection by Yakushima Macaques (*Macaca fuscata yakui*): The Influence of Food Availability and Temperature. *Int J Primatol* 16:611–627
- Alm U, Birgersson B, Leimar O (2002) The effect of food quality and relative abundance on food choice in fallow deer. *Anim. Behav.* 64:439–445
- Anderson MJ (2006) Distance based tests for homogeneity of multivariate dispersions. *Biometrics* 62:245–253
- Barraza JM, Montes JF, Martínez NH, Deloya C (2010) Assemblage of coprophagous beetles (Scarabaeidae: Scarabaeinae) of Tropical Dry Forest in Bahia Concha, Santa Marta (Colombia). *Rev Colomb Entomol* 36:285–291
- Beiroz W, Sayer E, Slade EM, Audino L, Braga RF, Louzada J, Barlow J (2018) Spatial and temporal shifts in functional and taxonomic diversity of dung beetle in a human-modified tropical forest landscape. *Ecol Indic* 95:418–526
- Bicknell JE, Phelps SP, Davies RG, Mann DJ, Struebig MJ, Davies ZG (2014) Dung beetles as indicators for rapid impact assessments: evaluating best forestry practice forestry in the Neotropics. *Ecol Indic* 43:154–161
- Birnie-Gauvin K, Peiman KS, Raubenheimer D, Cooke SJ (2017) Nutritional physiology and ecology of wildlife in a changing world. *Conserv Physiol* 5:1–18
- Bogoni JA, Hernández MIM (2014) Attractiveness of native mammal’s feces of different trophic guilds to dung beetles (Coleoptera: Scarabaeinae). *J Insect Sci* 14:299
- Borges SH (2004) Species poor but distinct: bird assemblages in white sand vegetation in Jaú National Park, Brazilian Amazon. *Ibis* 146:114–124
- Boulay R, Fedriani JM, Manzaneda AJ, Cerdá X (2005) Indirect effects of alternative food resources in an ant–plant interaction. *Plant Anim Interact* 144:72–79
- Bourg A, Escobar F, MacGregor-Fors I, Moreno CE (2016) Got dung? Resource selection by dung beetles in Neotropical forest fragments and cattle pastures. *Neotrop Entomol* 45:490–498
- Braga RF, Korasaki V, Andresen E, Louzada J (2013) Dung beetle community and functions along a habitat–disturbance gradient in the Amazon: a rapid assessment of ecological functions associated to biodiversity. *Plos One* 8:e57786
- Brown JH (1984) On the relationship between abundance and distribution of species. *Am Nat* 124:255–279
- Carvalho WD, Mustin K, Farneda FZ et al (2021) Taxonomic, functional and phylogenetic bat diversity decrease. *Oecologia* 197:223–239
- Chamorro-Florescano IA, Favila ME, Macías-Ordóñez R (2011) Ownership, size and reproductive status affect the outcome of food ball contests in a dung roller beetle: when do enemies share? *Evol Ecol* 25:277–289
- Chazdon RL, Chao A, Colwell RK, Lin SY, Norden N, Letcher SG, Clark DB, Finegan B, Arroyo JP (2011) A novel statistical method for classifying habitat generalists and specialists. *Ecology* 92:1332–1343
- Clarke KR, Gorley RN (2006) Primer v6 Permanova+. Primer-E Ltd, Plymouth, UK
- Climate-Data (2021) Climate data. Available from: <https://en.climate-data.org/>. Accessed 26 Nov 2021
- Correa CMA, da Silva PG, Puker A, Gil RL, Ferreira KR (2021) Rainfall seasonality drives the spatiotemporal patterns of dung beetles in Amazonian forests in the arc of deforestation. *J Insect Conserv* 25:453–463
- Correa CMA, Puker A, Korasaki V, Ferreira KR, Abot AR (2016) Attractiveness of baits to dung beetles in Brazilian savanna and exotic pasturelands. *Entomol Sci* 19:112–123
- Correa CMA, Salomão RP, Xavier BFS, Puker A, Ferreira KR (2023) Not all dung beetles feed on dung: Scarabaeinae (Coleoptera: Scarabaeidae) attracted to different carrion types in contrasting habitats at Brazilian Amazon. *Austral Ecol* 48. <https://doi.org/10.1111/aec.13312>
- Crawley M (2013) The R Book, 2nd edn. Wiley & Sons, London, UK
- Curtis RJ, Brereton TM, Dennis RLH, Carbone C, Isaac NJB (2015) Butterfly abundance is determined by food availability and is mediated by species traits. *J Appl Ecol* 52:1676–1684
- da Silva PG, Hernández MIM (2015) Spatial patterns of movement of dung beetle species in a tropical forest suggest a new trap spacing for dung beetle biodiversity studies. *PLoS One* 10:e0126112
- Dormont L, Epinat G, Lumaret JP (2004) Trophic preferences mediated by olfactory cues in dung beetles colonizing cattle and horse dung. *Environ Entomol* 33:370–377
- Dormont L, Jay-Robert P, Bessi ere JM, Rapior S, Lumaret JP (2010) Innate olfactory preferences in dung beetles. *J Exp Biol* 213:3177–3186
- Favila ME (2005) *Alpha and beta diversity of dung beetles (Scarabaeinae) at Los Tuxtlas, Mexico*. M3m: Monografias Tercer Milenio 4:209–219
- Ferreira KR, Puker A, Correa CMA (2020) The attraction of Amazonian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) to the feces of omnivorous mammals is dependent on their diet: implications for ecological monitoring. *Environ Entomol* 49:1383–1392
- Filgueiras BKC, Liberal CN, Aguiar CDM, Hernández MIM, Iannuzzi L (2009) Attractivity of omnivore, carnivore and herbivore mammalian dung to Scarabaeinae (Coleoptera, Scarabaeidae) in a Tropical Atlantic Rainforest remnant. *Rev Bras Entomol* 53:422–427
- Filgueiras BKC, Iannuzzi L, Leal IR (2011) Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest. *Biol Conserv* 144:362–369
- Filgueiras BKC, Peres CA, Iannuzzi L, Tabarelli M, Leal IR (2021) Recovery of dung beetle assemblages in regenerating Caatinga dry forests following slash-and-burn agriculture. *For Ecol Manag* 496:119423
- Fincher GT (1973) Nidification and reproduction of phanaeus spp. in three textural classes of soil (Coleoptera: Scarabaeidae). *Coleopt Bull* 27:33–37
- Frank K, Krell FT, Slade EM et al (2018) Global dung webs: high trophic generalism of dung beetles along the latitudinal diversity gradient. *Ecol Lett* 21:1229–1236
- Gaston KJ, Blackburn TM, Lawton JH (1997) Interspecific abundance–range size relationships: an appraisal of mechanisms. *J Anim Ecol* 66:579–601
- G enier F (2009) Le genre *Eurysternus* Dalman, 1824 (Scarabaeidae: Scarabaeinae, Oniticellini), r evision taxonomique et cl es de d etermination illustr ees. Sofia, Bulgaria: Pensoft Series Faunistica 85
- Gim enez G omez VC, Verd u JR, G omez-Cifuentes A, Vaz-de-Mello FZ, Zurita GA (2018) Influence of land use on the trophic niche

- overlap of dung beetles in the semideciduous Atlantic forest of Argentina. *Insect Conserv Diver* 11:554–564
- González-Alvarado A, Vaz-de-Mello FZ (2021) Towards a comprehensive taxonomic revision of the Neotropical dung beetle subgenus *Deltochilum* (*Deltohyboma*) Lane, 1946 (Coleoptera: Scarabaeidae: Scarabaeinae): Division into species-groups. *Plos One* 16:e0244657
- González-Megías A, Sánchez-Piñero F (2004) Resource limitation of nesting: chance favors the prepared dung beetle. *Environ Entomol* 33:188–196
- González-Solís J, Oro D, Jover L, Ruiz X, Pedrocchi V (1997) Trophic niche width and overlap of two sympatric gulls in the southwestern mediterranean. *Oecologia* 112:75–80
- Halffter G, Matthews EG (1966) The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Folia Entomol Mex* 12:1–312
- Halffter G, Halffter V (2009) Why and where coprophagous beetles (Coleoptera: Scarabaeinae) eat seeds, fruits or vegetable detritus. *Bol Soc Entomol Aragonesa* 45:1–22
- Hanski I, Koskela H (1977) Niche relations among dung-inhabiting beetles. *Oecologia* 8:203–231
- Hanski I (1990) Living in patchy environments. In: Shorrocks B, Swingland IR (eds) *Dung and carrion insects*. Oxford University Press, Oxford
- Hanski I, Cambefort Y (1991) *Dung Beetle Ecology*. Princeton University Press, Princeton
- Horgan FG (2008) Dung beetle assemblages in forests and pastures of El Salvador: a functional comparison. *Biodivers Conserv* 17:2961–2978
- Iannuzzi L, Salomão RP, Costa FC, Liberal CN (2016) Environmental patterns and daily activity of dung beetles (Coleoptera: Scarabaeidae) in the Atlantic Rainforest of Brazil. *Entomotropica* 31:196–207
- Junk WJ, Piedade MTF, Schöngart J, Cohn-Haft M, Adeney JM, Wittmann F (2011) A Classification of major naturally-occurring Amazonian lowland Wetlands. *Wetlands* 31:623–640
- Komonen A, Grapputo A, Kaitala V, Kotiaho JS, Päävinen J (2004) The role of niche breadth, resource availability and range position on the life history of butterflies. *Oikos* 105:41–54
- Krebs J, Davies N (1981) *An introduction to behavioural ecology*. Blackwell Scientific Publications, London
- Larsen TH, Forsyth A (2005) Trap spacing and transect design for dung beetle biodiversity studies. *Biotropica* 37:322–325
- Larsen TH, Lopera A, Forsyth A (2006) Extreme trophic and habitat specialization by Peruvian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Coleopt Bull* 60:315–324
- Lemke TO (1984) Foraging ecology of the long-nosed bat, *Glossophaga soricina*, with respect to resource availability. *Ecology* 65:538–548
- Liberal CN, Farias AMI, Meiado MV, Figueiras BKC, Iannuzzi L (2011) How habitat change and rainfall affect dung beetle diversity in Caatinga, a Brazilian semi-arid ecosystem. *J Insect Sci* 11:1–11
- Massei G, Genov PV, Staines BW (1996) Diet, food availability and reproduction of wild boar in a Mediterranean coastal area. *Acta Theriologica* 41:307–320
- Medina AM, Lopes PP (2014) Resource utilization and temporal segregation of Scarabaeinae (Coleoptera, Scarabaeidae) community in a Caatinga fragment. *Neotrop Entomol* 43:127–133
- Nandintsetseg D, Bracis C, Leimgruber P et al (2019) Variability in nomadism: environmental gradients modulate the movement behaviors of dryland ungulates. *Ecosphere* 10:e02924
- Noriega JA, Calle JC (2008) Consumption of *Gustavia hexapetala* (Aublet) Smith (Lecythidales: Lecythidaceae) by the dung beetle *Eurysternus plebejus* Harold (Coleoptera: Scarabaeidae). *The Coleopterists Bulletin* 62:455–460
- Noriega JA (2012) Dung Beetles (Coleoptera: Scarabaeinae) Attracted to *Lagothrix lagothricha* (Humboldt) and *Alouatta seniculus* (Linnaeus) (Primates: Atelidae) Dung in a Colombian Amazon Forest. *Psyche* 2012:1–6
- Noriega JA (2015) How a locality can have so many species? A case study with dung beetles (Coleoptera: Scarabaeinae) in a tropical rain forest in Colombia. In: Stack C (ed) *Beetles: biodiversity, ecology and role in the environment*. Nova Science Publishers, New York
- Nosil P (2002) Food fights in house crickets, *Acheta domesticus*, and the effects of body size and hunger level. *Can J Zool* 80:409–417
- Oksanen J, Simpson GL, Blanchet FG et al (2020) *Vegan: community ecology package*. Available from: <https://cran.r-project.org/web/packages/vegan/vegan.pdf>. Accessed 16 Feb 2022
- Paine TD, Birch MC, Svihra P (1981) Niche breath and resource partitioning by four sympatric species of bark beetles (Coleoptera: Scolytidae). *Oecologia* 48:1–6
- Panizzi AT (2000) Suboptimal Nutrition and Feeding Behavior of Hemipterans on Less Preferred Plant Food Sources. *An Soc Entomol Bras* 29:1–12
- Ponce-Santizo G, Andresen E, Cano E (2006) Dispersión primaria de semillas por primates y dispersión secundaria por escarabajos coprófagos en Tikal, Guatemala. *Biotropica* 38:390–397
- Puker A, Correa CMA, Butzke L, Pacheco RA (2021) Using aerial fruit-baited traps with diferente naturally fermented baits to survey scarab beetles in the Amazon rainforest. *Stud Neotrop Fauna Environ* 56:238–243
- R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna
- Raine EH, Slade EM (2019) Dung beetle–mammal associations: methods, research trends and future directions. *Proc R Soc B* 286:20182002
- Ratcliffe BC (2013) The dung- and carrion-feeding scarabs (Coleoptera: Scarabaeoidea) OF an Amazonian blackwater rainforest: results of a continuous, 56-week, baited-pitfall trap study. *Coleopt Bull* 67:481–520
- Rivera JD, Favila ME (2022) Good news! Sampling intensity needed for accurate assessments of dung beetle diversity may be lower in the Neotropics. *Front Ecol Evol* 10:999488
- Rougon D, Rougon C (1991) Dung beetles of the Sahel region. In: Hanski I, Cambefort Y (eds) *Dung beetle ecology*. Princeton University Press, Princeton
- Sailer LD, Gaulin SJC, Boster JS, Kurland JA (1985) Measuring the relationship between dietary quality and body size in primates. *Primates* 26:14–27
- Salomão RP, Iannuzzi L (2017) How do regeneration stages of Caatinga forests influence the structure of dung beetle (Coleoptera: Scarabaeidae) assemblage? *Coleopt Bull* 71:578–588
- Salomão RP, Maia ACD, Bezerra BM, Iannuzzi L (2017) Attractiveness of different food resources to dung beetles (Coleoptera: Scarabaeidae) of a dry Tropical area. *Neotrop Entomol* 47:69–78
- Salomão RP, Cerqueira LV-BMP, Gomes AAC, González-Tokman D, Maia ACD, Iannuzzi L (2022) Dung or carrion? Sex and age determine resource attraction in dung beetles. *Ecol Entomol* 47:52–62
- Salomão RP, Pires DA, Baccaro FB, Schietti J, Vaz-de-Mello FZ, Lima AP, Magnusson WE (2022) Water table level and soil texture are important drivers of dung beetle diversity in Amazonian lowland forests. *App Soil Ecol* 170:104260
- Sánchez-Bermejo PC, deCastro-Arrazola I, Cuesta E, Davis ALV, Moreno CE, Sánchez-Piñero F, Hortal J (2022) Aridity drives the loss of dung beetle taxonomic and functional diversity in three contrasting deserts. *J Biogeogr* 49:2243–2255
- Sarkar D (2021) Package ‘lattice’. Available from: <https://cran.r-project.org/web/packages/lattice/lattice.pdf>. Accessed 16 Feb 2022
- Scholtz CH, Davis ALV, Kryger U (2009) *Evolutionary biology and conservation of dung beetles*. Pensoft Publishers, Sofia

- Schmitt T, Krell FT, Linsenmair KE (2004) Quinone mixture as attractant for necrophagous dung beetles specialized on dead millipedes. *J Chem Ecol* 30:731–740
- Seixas RR, Santos SE, Okada Y, Freitas AVL (2017) Population biology of the sand forest specialist butterfly *Heliconius hermathena hermathena* (Hewitson) (Nymphalidae: Heliconiinae) in Central Amazonia. *J Lepidopterists' Soc* 71:133–140
- Servín-Pastor M, Salomão RP, Caselín-Cuevas F et al (2021) Malnutrition and parasitism shape ecosystem services provided by dung beetles. *Ecol Indic* 121:107205
- Sexton JP, Montiel J, Shay JE, Stephens MR, Slatyer RA (2017) Evolution of ecological niche breadth. *Annu Rev Ecol Evol Syst* 48:183–206
- Silva RJ, Ribeiro HV, Souza MF, Vaz-de-Mello FZ (2015) Influence of soil granulometry on the structure of functional guilds of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) at semidecious forests in the state of Mato Grosso, Brazil. *Biosc J* 31:601–612
- Stavert JR, Drayton BA, Beggs JR, Gaskett AC (2014) The volatile organic compounds of introduced and native dung and carrion and their role in dung beetle foraging behaviour. *Ecol Entomol* 39:556–565
- Swihart RK, Gehring TM, Kolozsvary MB, Nupp TE (2003) Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. *Divers Distrib* 9:1–18
- Tocco C, Dacke M, Byrne M (2021) The finely defined shift work schedule of dung beetles and their eye morphology. *Ecol Evol* 11:15947–15960
- Vaz-de-Mello FZ (2008) Synopsis of the new subtribe *Scatimina* (Coleoptera: Scarabaeidae: Scarabaeinae: Ateuchini), with descriptions of twelve new genera and review of *Genieridium*, new genus. *Zootaxa* 1955:1–75
- Vaz-de-Mello FZ, Edmonds WD, Ocampo FC, Schoolmeesters PA (2011) A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Coleoptera: Scarabaeidae). *Zootaxa* 2854:1–73
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.