

Water table level and soil texture are important drivers of dung beetle diversity in Amazonian lowland forests

Renato Portela Salomão^{a,*}, Diego de Alcântara Pires^a, Fabricio Beggiato Baccaro^b, Juliana Schietti^b, Fernando Zagury Vaz-de-Mello^c, Albertina Pimentel Lima^a, William Ernest Magnusson^a

^a Instituto Nacional de Pesquisas da Amazônia, Programa de Pós-Graduação em Ecologia, Av. André Araújo 2936, Manaus, Amazonas 69060-001, Brazil

^b Universidade Federal do Amazonas, Departamento de Biologia, Av. Gen. Rodrigo Octávio 6200, Manaus, Amazonas 69080-900, Brazil

^c Universidade Federal de Mato Grosso, Departamento de Biologia e Zoologia, Instituto de Biotecnologia, Av. Fernando Corrêa da Costa 2367, Cuiabá, Mato Grosso 78060-900, Brazil

ARTICLE INFO

Keywords:

Neotropics
Scarabaeinae
Soil granulometry
Tropical rainforest

ABSTRACT

The high biodiversity of the Amazon region is related to variation in soil physical properties and water-table depths. Dung beetles are efficient bioindicators that feed and breed on the soil surface and below ground, affecting soil properties and being affected by them. Here, we investigate the influence of soil physical characteristics (proportions of sand, silt, clay) and water-table depth on dung beetle assemblages and functional groups in a forest in central Amazonia. We sampled beetles in 29 transects with different soil physical properties and water-table maximum levels, and analyzed beetle species richness, abundance and species composition for the total assemblage and for each functional group (rollers, tunnellers, dwellers). Dung beetle abundance increased with soil clay content (GLMM; $p = 0.009$) whereas dweller (GLMM; $p = 0.017$) and tunneller species richness increased with clay and silt contents (GLMM; $p = 0.018$). Sites with deeper water table had greater roller-beetle abundance (GLMM; $p = 0.049$). Dung beetle assemblage composition was strongly influenced by clay content. Our results suggest that soil texture and water-table levels determine dung beetle distributions, both for the whole assemblages and for each functional group separately. These findings highlight the role of soil structure in determining dung beetle assemblages.

1. Introduction

Water-table depth and soil properties play a crucial role in the establishment and maintenance of ecological communities that live in the soil (Hayashi and Rosenberry, 2002; Huerta and van-der-Wall, 2012; Li et al., 2020). Soil granulometry (i.e. proportions of silt, clay, and sand) may result in different microhabitat conditions, sustaining species with specific habitat requirements (Hayashi and Rosenberry, 2002; Powers et al., 2009; Weltzin et al., 2000). For example, tropical sandy soils are physically and chemically constraining, because they have low nutrient-holding capacity and are less prone to compaction under anthropic pressure (Blanchart et al., 2007). In contrast, soils with high amounts of clay and low bulk density may retain moisture for longer periods (Powers et al., 2009). In the tropical forests of Mexico, for example, the diversity of flies, earthworms, and beetles are positively related to the

proportion of silt in soils (Huerta and van-der-Wall, 2012).

Dung beetles (Coleoptera: Scarabaeinae) are sensitive to changes in the environment (Favila and Halfpeter, 1997; Gardner et al., 2008a, 2008b; Nichols et al., 2007). Food resources for dung beetles are scarce and unpredictably distributed in nature, resulting in fierce competition for food (Hanski and Koskela, 1977; Scholtz et al., 2009). As a consequence, dung beetles have developed different resource-removal strategies that may relate with edaphic factors. Dung beetle species are classified as rollers (roll food balls to use for feeding and breeding), tunnellers (build tunnels in which they drag food to construct their breeding balls), or dwellers (feed and breed directly in the food resource) (Halfpeter and Edmonds, 1982; Hanski and Cambefort, 1991; Scholtz et al., 2009). Each resource-removal strategy encompasses a set of specific types of behavior and interactions between the dung beetles and the environment (Doubt, 1990; Halfpeter and Edmonds, 1982). In

* Corresponding author.

E-mail address: renatopsaloma3@hotmail.com (R.P. Salomão).

<https://doi.org/10.1016/j.apsoil.2021.104260>

Received 28 April 2021; Received in revised form 1 October 2021; Accepted 5 October 2021
0929-1393/© 2021 Elsevier B.V. All rights reserved.

addition, resource-removal strategies are used to define functional groups of dung beetles; therefore, by studying these groups it is possible to have a finer comprehension of beetle ecological response to environmental pressures (e.g. Barragán et al., 2011; Nunes et al., 2016; Salomão et al., 2019).

By digging tunnels and moving decomposing organic matter into the soil, dung beetles improve soil quality, promoting soil aeration and nutrient cycling (Nichols et al., 2008). Through such behaviors, dung beetles actively modify soil structure and properties (Arellano et al., 2018), but soil properties can also determine distributions of dung beetle assemblages. Feeding and breeding of dung beetles take place mostly on the soil surface and below ground (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991; Scholtz et al., 2009). Therefore, soil structure and water-table levels may determine the spatial distribution of dung beetle assemblages, and such effects probably vary depending on the resource-removal strategy of the beetle species. Tunneller beetles dig deep tunnels, which may be a few centimeters to more than one meter deep (Halffter and Edmonds, 1982; Scholtz et al., 2009). Dwellers nest within or immediately under the dropping, while rollers roll portion of the dung away and bury it at some distance from the dropping (Halffter and Edmonds, 1982; Scholtz et al., 2009). Therefore, soil properties may affect dung beetle diversity (e.g. Farias et al., 2015; Silva et al., 2015), and tunneller-beetle diversity and roller abundance are sometimes greater in more sandy soils (Davis, 1996a; Farias and Hernández, 2017). Nonetheless, clay content can be an important driver of dung beetle diversity in tropical and subtropical ecosystems (Davis, 1996a, 1996b; Farias and Hernández, 2017; Silva et al., 2015). There is little information regarding dung beetle response to water-table depth (Brussaard, 1985), but sites with shallow water table and waterlogged soils could restrain beetle tunneling activity (Osberg et al., 1994). To our knowledge, there are no studies that analyzed the effects of both soil properties and water-table levels on dung beetle diversity.

In the Amazon region, high biodiversity is found in regions with large variations in soil physical properties and water-table depths (Sombroek, 2000). Different proportions of sand and clay, together with different water-table depths, allow the establishment of distinct vegetation physiognomies in the Amazon, such as “campina” and “terra firme” forests, consequently comprising different ecological communities (Junk et al., 2011; Sombroek, 2000). Areas with high water table comprise a large part of Amazonian tropical forests (Rennó et al., 2008; Sombroek, 2000), and these coincide with the distributions of many species, including plants (Drucker et al., 2008; Schiatti et al., 2014), ants (Baccaro et al., 2013; de Souza Holanda et al., 2020), and bats (do Amaral Pereira et al., 2019). In addition, areas with contrasting soil and water-table properties sustain ecological communities with different tolerances to anthropogenic disturbances (Moran and Mauseel, 2002; Santos et al., 2020; Villa et al., 2018). In the Amazon region, deforestation due to human activities (e.g. agriculture expansion and dam construction) strongly alters soil and water-table dynamics, and indirectly biodiversity (Benchimol and Peres, 2015; Moran and Mauseel, 2002; Santos et al., 2020; Silva et al., 2017). Therefore, in order to understand the biodiversity of the Amazon region, it is crucial to determine how soil properties and water-table depth modulate its biodiversity.

In this study, we assessed the effects of soil physical properties (i.e. proportions of sand, silt and clay) and water-table maximum level on characteristics of dung beetle assemblages (species richness, abundance, and species composition) in the central Amazon. Previous studies have shown that soil texture affects the ability of dung beetles to gather food and construct nests (Farias and Hernández, 2017; Jay-Robert et al., 2008; Scholtz et al., 2009). Therefore, compacted soils and high water tables could limit their spatial distribution. In addition, tunneller dung beetles construct their nests beneath or near the food source (Halffter and Edmonds, 1982). Since softer sandy soils are considered easier to tunnel than clay (Hanski and Cambefort, 1991), we predicted that sandy soils could sustain more diverse assemblages than soils with higher clay and silt contents. In addition, we expected that high water tables might

limit the available soil for nesting, especially for tunneller dung beetles (Halffter and Edmonds, 1982). Therefore, species distributions may also be limited in areas with high water table, allowing only subsets of the dung beetle assemblages that occur in sites with low water tables.

2. Material and methods

2.1. Study area

The study was carried out in four research sites along a 200 km transect in the Purus–Madeira interfluvium, south of the Amazon River in central Amazonia. The research sites were distributed at ~50 km intervals along the BR-319 highway, parts of which have been impassable for regular traffic due to flooding since 1988 (Fearnside and Graça, 2006).

The Purus–Madeira interfluvium is predominantly flat, with elevation ranging from ~30 to ~80 m (Sombroek, 2000). This region is part of the Amazon basin ‘loamy plains’ (Sombroek, 2000) that covers approximately 11% of the Amazon basin. Soils are mainly Gleysols and Plinthosols with poor drainage, and the predominant texture is silt to fine sand (Sombroek, 2000). Large areas are waterlogged during the rainy season, and many of the small streams dry during the dry season. The water table is within 7 m of the surface throughout the year in most of the region, and some areas are flooded for short periods (~50 cm) when the water-table reaches the highest levels in the rainy season (Schiatti et al., 2016). Mean annual precipitation varied from 2000 to 2400 mm based on a combination of long and short-term meteorological stations from 1965 to 1990 (Sombroek, 2001). The vegetation is classified as lowland dense rainforest in the north and lowland open rainforest dominated by palms in the south (BRASIL, 1974). For more details about vegetation structure and water-table variation, see Schiatti et al. (2016).

2.2. Sampling design

The study was carried out in 29 transects nested in three sites (i.e. sampling modules) along 200 km of the BR-319 highway. In each site, 10 transects were regularly distributed 1 km apart (except in one site, which had 9 transects), along two 5 km trails (Magnusson et al., 2013). The 250 m-long transects follow the terrain altitudinal contour lines to minimize topo-edaphic and water-table depth variation within transects (Magnusson et al., 2005). Transects were established at least 1 km from the road to avoid secondary forests.

We collected dung beetles in November and December 2015, at the beginning of the rainy season. We captured dung beetles in each transect in six baited pitfall traps placed at 50 m intervals. The pitfalls consisted of 500 ml plastic vials buried to ground level and partially filled with 70% alcohol. We used ~20 g of fresh human feces as bait in each trap, and the pitfalls were left open for 48 h. Subsequently, we removed the dung beetles and stored them in alcohol for identification. A total of 174 pitfall traps were used in this study. We used the key by Vaz-de-Mello et al. (2011) to identify dung beetles to genus. Material in the entomological collection of the Universidade Federal do Mato Grosso – UFMT was used as reference for species identification. Voucher specimens were deposited in the entomological collections of UFMT and the Instituto Nacional de Pesquisas da Amazônia – INPA. Species were also classified according to their resource-removal strategies (i.e. rollers, tunnellers, or dwellers), which is one of the most common functional-group classifications for dung beetles (Barragán et al., 2011; Halffter and Edmonds, 1982; Nunes et al., 2016; Salomão et al., 2019).

2.3. Soil texture

In each transect, six soil samples (30 cm × 30 cm × 5 cm) were obtained with the aid of a shovel, after removing litterfall and roots. The soil samples were regularly distributed (every 50 m) along the transects. The six soil samples were mixed to form one sample per transect, from

Table 1

Dung beetle species recorded in 29 sampling sites on the BR319, northern interfluvium of Purus and Madeira rivers, Amazonas state, Brazil. T – tunneller; R – roller; D – dweller.

Species	Resource Removal Strategy	Total abundance	Relative abundance (%)	No of sites where species was recorded
<i>Dichotomius podalirius</i>	T	395	10.13	20
<i>Dichotomius mamillatus</i>	T	88	2.26	19
<i>Dichotomius nimuendaju</i>	T	2	0.05	2
<i>Dichotomius worontzowi</i>	T	1	0.03	1
<i>Dichotomius batesi</i>	T	77	1.98	19
<i>Dichotomius aff. Lucasi</i>	T	52	1.33	17
<i>Dichotomius robustus</i>	T	15	0.38	10
<i>Dichotomius apicalis</i>	T	31	0.80	12
<i>Dichotomius sp</i>	T	1	0.03	1
<i>Deltochilum orbiculare</i>	R	32	0.82	12
<i>Deltochilum orbigny</i>	R	28	0.72	20
<i>Deltochilum amazonicum</i>	R	28	0.72	20
<i>Deltochilum carinatum</i>	R	1	0.03	1
<i>Deltochilum sp1</i>	R	118	3.03	4
<i>Deltochilum sp2</i>	R	63	1.62	15
<i>Deltochilum sp3</i>	R	40	1.03	20
<i>Scybalocanthon sp</i>	R	43	1.10	16
<i>Silvicanthon sp. nv</i>	R	4	0.10	4
<i>Canthon triangularis</i>	R	8	0.21	5
<i>Canthon fulgidus</i>	R	46	1.18	6
<i>Canthon semiopacus</i>	R	5	0.13	4
<i>Canthon sp</i>	R	1	0.03	1
<i>Sylvicanthon proseni</i>	R	328	8.41	26
<i>Ateuchus substriatus</i>	T	56	1.44	21
<i>Ateuchus murrayae</i>	T	425	10.90	27
<i>Ateuchus cf. pygidialis</i>	T	2	0.05	2
<i>Ateuchus cf. scatimoides</i>	T	2	0.05	2
<i>Ateuchus cf. candezei</i>	T	9	0.23	7
<i>Ateuchus sp1</i>	T	22	0.56	1
<i>Ateuchus sp2</i>	T	2	0.05	2
<i>Canthidium funebre</i>	T	3	0.08	2
<i>Canthidium orbiculatum</i>	T	16	0.41	1
<i>Canthidium sp1</i>	T	1	0.03	1
<i>Canthidium sp2</i>	T	5	0.13	3
<i>Canthidium sp3</i>	T	4	0.10	4
<i>Canthidium sp4</i>	T	29	0.74	10
<i>Eurysternus cayennensis</i>	D	823	21.11	28
<i>Eurysternus caribaeus</i>	D	151	3.87	22
<i>Eurysternus foedus</i>	D	12	0.31	9
<i>Eurysternus hamaticollis</i>	D	11	0.28	3
<i>Eurysternus hypocrita</i>	D	105	2.69	24
<i>Eurysternus wittmerorum</i>	D	91	2.33	20
<i>Eurysternus arnaudi</i>	D	81	2.08	20
	D	23	0.59	13

Table 1 (continued)

Species	Resource Removal Strategy	Total abundance	Relative abundance (%)	No of sites where species was recorded
<i>Eurysternus strigilatus</i>				
<i>Eurysternus vastiorum</i>	D	2	0.05	1
<i>Coprophanaeus telamon</i>	T	13	0.33	10
<i>Phanaeus bispinus</i>	T	2	0.05	2
<i>Phanaeus cambeforti</i>	T	10	0.26	7
<i>Phanaeus chalcomelas</i>	T	48	1.23	17
<i>Oxysternon conspicillatum</i>	T	5	0.13	4
<i>Oxysternon silenus</i>	T	13	0.33	4
<i>Onthophagus rubrescens</i>	T	236	6.05	23
<i>Onthophagus clypeatus</i>	T	1	0.03	1
<i>Onthophagus onorei</i>	T	151	3.87	20
<i>Onthophagus osculatii</i>	T	165	4.23	21

which 500 g was used to estimate soil texture. The 500 g of homogenized soil samples was dried at 105 °C for 24 h and sieved using a 2 mm mesh. The amounts of sand, silt, and clay content for each transect was converted to proportions in further analyses. All soil analyses were done in the Laboratório Temático de Solos e Plantas at INPA (for a detailed description of the methods, see [PPBio, 2020](#)).

2.4. Water-table level

A 7.5 m piezometer tube was installed in each transect, with approximately 7 m below and 0.5 m above ground level. The piezometer was custom-made and consisted of a 6 cm diameter plastic pipe with holes drilled in the lower portion (30 cm) to allow water flow. The holes were covered with a mesh to avoid obstruction by mud, and the piezometers were capped to prevent entry of rainwater and litter. A lateral orifice equilibrated the air pressure in the pipe and allowed water column movement. Between March 2011 and April 2013, the water-table level was manually monitored in all plots. We used the groundwater maximum level (i.e. the registered water table level closest to the soil surface) as a measure of disturbance caused by the water table on dung beetle assemblages. We opted for this metric, rather mean level, because we sampled dung beetles during the rainy season and the maximum level is more related to unpredictable flooding. Also, the maximum water-table level is probably more biologically meaningful since this restricts the soil layer available for nesting by dung beetles.

2.5. Data analysis

The effects of soil texture and water-table maximum level on dung beetle diversity (observed and estimated species richness) and abundance were analyzed with Generalized Linear Mixed Models (GLMMs) for observed species richness and abundance, and linear mixed models (LMMs) for estimated species richness. Soil sand content was correlated with clay (Pearson- $r = -0.58$) and silt content (Pearson- $r = -0.72$) and could not be included in the same model. Clay and silt proportions were weakly correlated (Pearson- $r = 0.3$) and were used to represent soil texture in the linear models (Table S1). We estimated species richness using the Chao 1 estimator, which is one of the simplest and most widely-used estimators ([Gotelli and Colwell, 2011](#)). For GLMMs and LMMs, sampling module was included as a random effect, and the soil

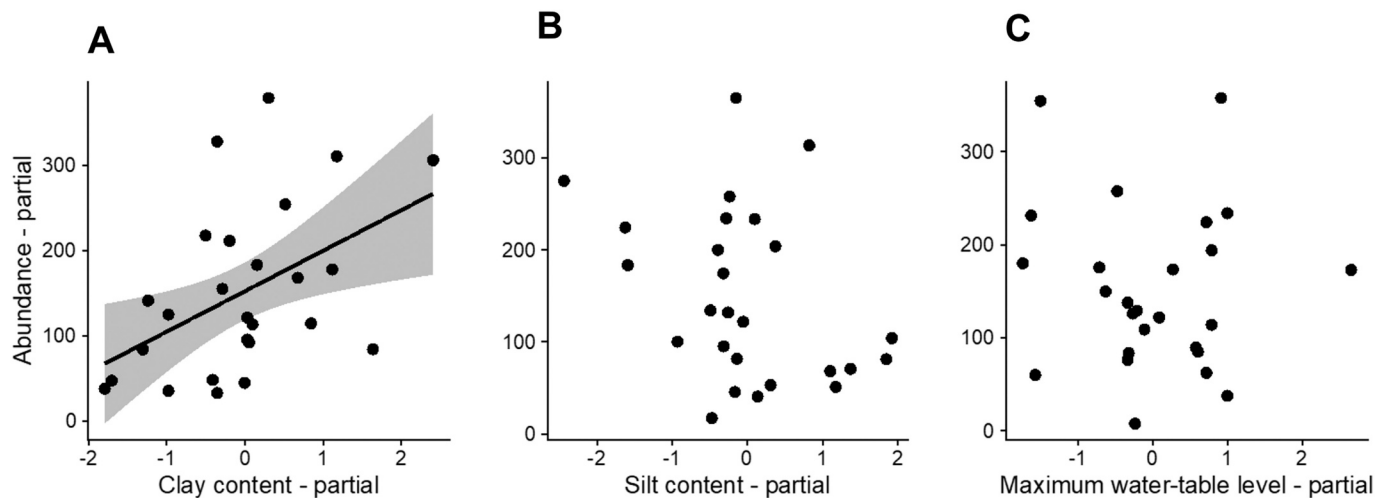


Fig. 1. Relationship between proportions of clay (A), and silt (B), maximum water-table level (C) and dung-beetle abundance in 29 sampling sites on the BR319, northern interfluvies of Purus and Madeira rivers, Amazonas state, Brazil.

Table 2

Summary of statistical models investigating the influence of soil texture (proportions of clay and silt) and water-table maximum level on observed and estimated species richness, for total dung beetle abundance and each functional group. Significant effects are shown in bold. Model parameters of observed species richness metrics were omitted because the null model had a better fit than the full model. For these groups the conditional R^2 values represent the variance explained by the random factor (module) only.

Diversity metric	R^2 Conditional	Fixed factor	<i>b</i>	<i>p</i> -Value
Abundance				
All assemblage	0.316	Clay	47.39	0.009
		Silt	-32.60	0.061
		Max. water table	-6.87	0.705
Dweller	0.325	Clay	17.94	0.017
		Silt	-12.63	0.079
		Max. water table	-7.18	0.337
Roller	0.133	Clay	0.18	0.237
		Silt	-0.21	0.189
		Max. water table	0.23	0.049
Tunneller	0.365	Clay	22.32	0.018
		Silt	-16.80	0.063
		Max. water table	-11.35	0.229
Observed species richness				
All assemblage	0.050	-	-	-
Dweller	0.253	-	-	-
Roller	0.117	-	-	-
Tunneller	0.162	-	-	-
Estimated species richness				
All assemblage	0.093	-	-	-
Dweller	0.236	Clay	-0.20	0.547
		Silt	-0.78	0.013
		Max. water table	0.29	0.372
Roller	0.250	-	-	-
Tunneller	0.322	Clay	2.78	0.012
		Silt	-0.35	0.738
		Max. water table	0.98	0.373

texture and water-table maximum level were the fixed variables. We built GLMMs and LMMs for assemblages of all dung beetle species and for each functional group separately (i.e. tunnellers, rollers, and dwellers). GLMMs used the Poisson error distribution or the negative-binomial error distribution (in the models with overdispersion). To validate the model fit, we compared the Akaike's Information Criterion (AIC) of each model with the respective AIC of the null model (intercept and random effect only). Full GLMM or LMM models were selected when the delta AIC (difference between full and null models) were >2 (Akaike, 1982). We calculated the conditional R^2 for each model, which

gives the variation explained by fixed and random effects in the model (Nakagawa and Schielzeth, 2013). The normality of residuals of the models was analyzed visually from normal q-q plots. Data were analyzed in R software version 3.2.0 (R Core Development Team, 2015).

To test the hypotheses that soil texture and water-table level influence overall assemblage composition, we used a multivariate approach that uses a Generalized Linear Model (GLM) to evaluate habitat-assemblage relationships across all species (Wang et al., 2012). The *manyglm* function in the R package 'mvabund', fits individual GLMs to each species and combines the results in an "assemblage" response (Wang et al., 2012). The major advantage of this procedure is the use of Poisson or negative-binomial error distribution to properly model the variance in the data (Wang et al., 2012). To check for structure in the residuals related to our sampling design (plots, nested in modules) (Dormann et al., 2007), we estimated *P* values from 999 bootstrap resamples and tested for spatial autocorrelation in community diversity using a Moran's I test on the summed residuals from the *manyglm* model. All *manyglm* models were fitted with negative-binomial error distributions.

To examine ecological correlates of dung beetle distribution patterns, we also ran the GLM multivariate approach (*manyglm*) for the species composition of the three functional groups (tunnellers, rollers, and dwellers). This classification is related to resource use, and potentially links species occurrence and environmental predictors at the assemblage level. To show the relationships between species distribution and environmental predictors we constructed compound graphs of species occurrence ordered by the predictors.

3. Results

A total of 3898 dung beetles belonging to 54 species and 12 genera were collected, *Dichotomius* and *Eurysternus* were the most diverse genera, with nine species recorded in each taxon (Table 1). Tunnellers comprised the most speciose group, with 32 species recorded, followed by rollers (13) and dwellers (9). The species with the most individuals recorded were *Eurysternus cayannensis*, *Ateuchus murryae* and *Dichotomius podalirius*, which together accounted for 42.14% of beetle individuals collected. Thirty-three species were rarely collected (i.e. relative abundance in collections $<1\%$), of which six were singletons and six doubletons (Table 1).

Dung beetle abundance was positively related to clay content (Fig. 1), but it had no statistically significant relationship with silt or water-table level. However, the probability associated with the null hypothesis for silt was low (Table 2), indicating a possible type-II error.

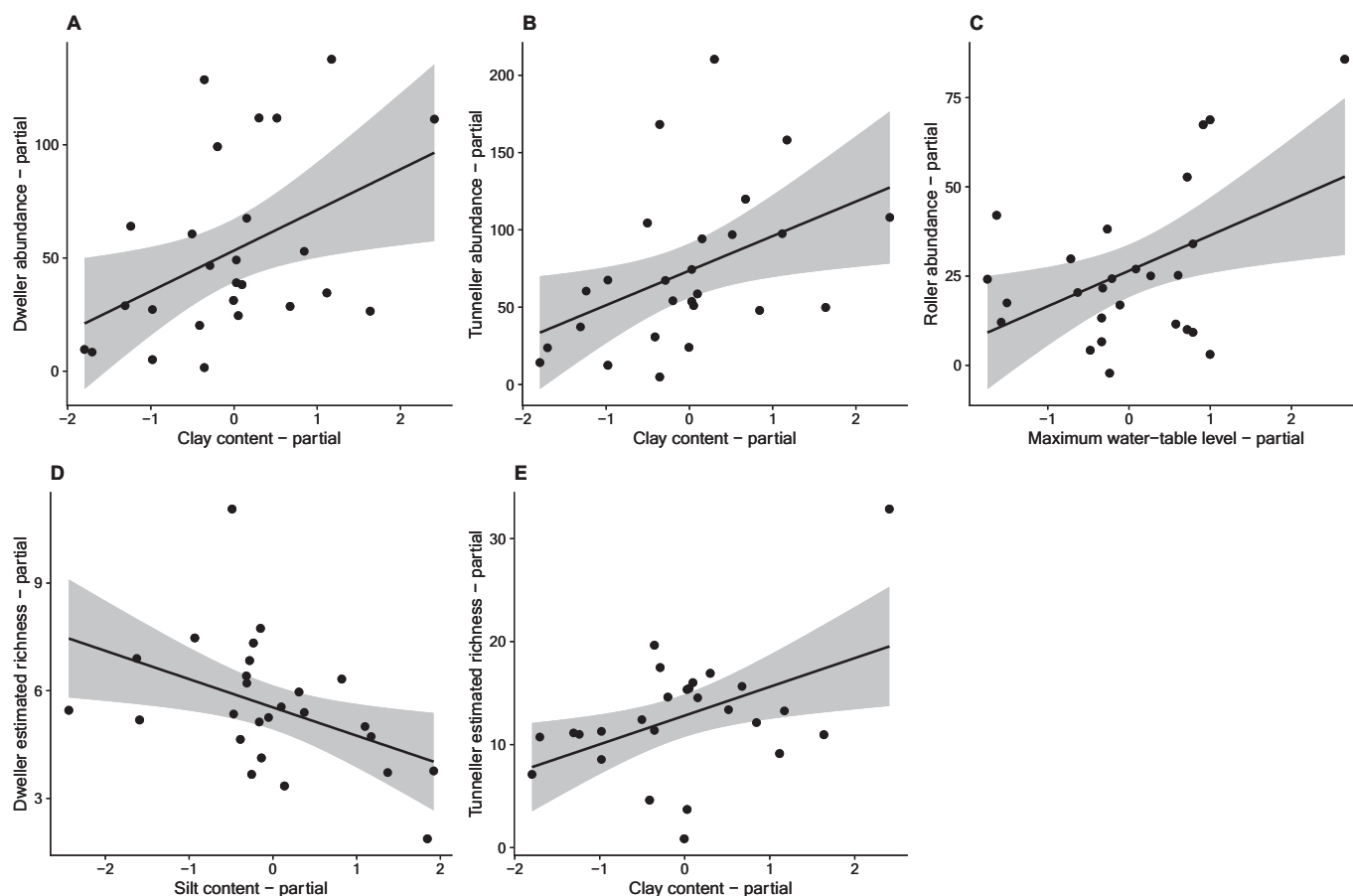


Fig. 2. Relationships between proportions of clay, and silt, maximum water-table level on dweller (A), tunneller (B), and roller abundance (C); and between dweller (D) and tunneller expected species richness (E) in 29 sampling sites on the BR319, northern interfluvium of Purus and Madeira rivers, Amazonas state, Brazil.

There were more dweller and tunneller beetles in soils with greater proportions of clay (Fig. 2A-B) and the abundance of roller beetles was higher in sites with deeper water-table maximum level (Fig. 2C). None of the predictors was related to observed species richness or estimated species richness of the overall assemblage (Table 2). Among functional groups, there was higher estimated species richness of dweller and tunneller dung beetles in sites with higher amounts of silt (Fig. 2D) and clay (Fig. 2E), respectively.

Considering the overall beetle assemblage of this study, there was an exponential relationship between species abundance and the number of transects in which they were recorded ($R^2 = 0.79$). The three most abundant species in each functional group (tunneller: *A. murryae*; roller: *Sylvicanthon proseni*; dweller: *E. cayannensis*) were the most widely distributed species in this study, occurring in at least 26 of the 29 transects (Table 1). Although being widely distributed in the study landscape, these species showed contrasting abundance patterns in relation to soil physical properties. The most abundant and widely distributed species, *E. cayannensis*, had a relatively more even distribution in soils with different proportions of silt and clay than the other dominant species (Fig. 3A). The dominant tunneller species, *A. murryae*, had highest abundances in soils with intermediate proportions of silt and clay (Fig. 3A). *Sylvicanthon proseni* had highest abundance in soils with low and high proportions of clay, and lower abundances in sites with intermediate proportions of clay (Fig. 3A).

Dung beetle species composition was related to the proportion of clay, silt and water-table maximum level (Table 3). Clay content had a stronger relationship with dung beetle-assemblage composition than the other predictor variables (Fig. 3A). There were more species restricted to soils with lower and higher clay content, compared with lower and

higher areas of maximum water-table level, or silt content (Fig. 3). This pattern was not consistent among functional groups. Dweller species composition was not related to any predictor, while rollers were related only to clay content. Tunnellers behaved as the overall assemblage, showing consistent species composition changes along clay, silt and maximum-water-table level gradients (Table 3).

4. Discussion

Understanding how ecological communities respond to shifts in soil properties, such as soil texture and water-table level, help us to understand how spatial variation in these resources may affect species distributions. No previous study analyzed the effect of soil texture and water-table level on Amazonian dung beetles, a group that is strongly affected by soil characteristics (Halffter and Edmonds, 1982). Our results indicate that soil properties and water-table level are better predictors of dung beetle species composition than univariate measures of diversity (richness and abundance). With few exceptions, the same overall patterns were obtained for different functional groups.

Dung beetle nesting behavior is closely related to the characteristics of the soil in which they build nests and prepare breeding balls (Halffter and Edmonds, 1982). In the Neotropics, dung beetle assemblages are dominated mostly by tunneller species, followed by rollers and dwellers (e.g. Cajaiba et al., 2017; Farias and Hernández, 2017; Hanski and Cambefort, 1991; Silva et al., 2015). Dominant dung beetle species in the Atlantic rainforest tend to have generalist feeding (Filgueiras et al., 2009), temporal (Iannuzzi et al., 2016) and spatial patterns (Filgueiras et al., 2011), suggesting a high tolerance to different environmental conditions. In our study, the most abundant species (e.g. *A. murryae*, *D.*

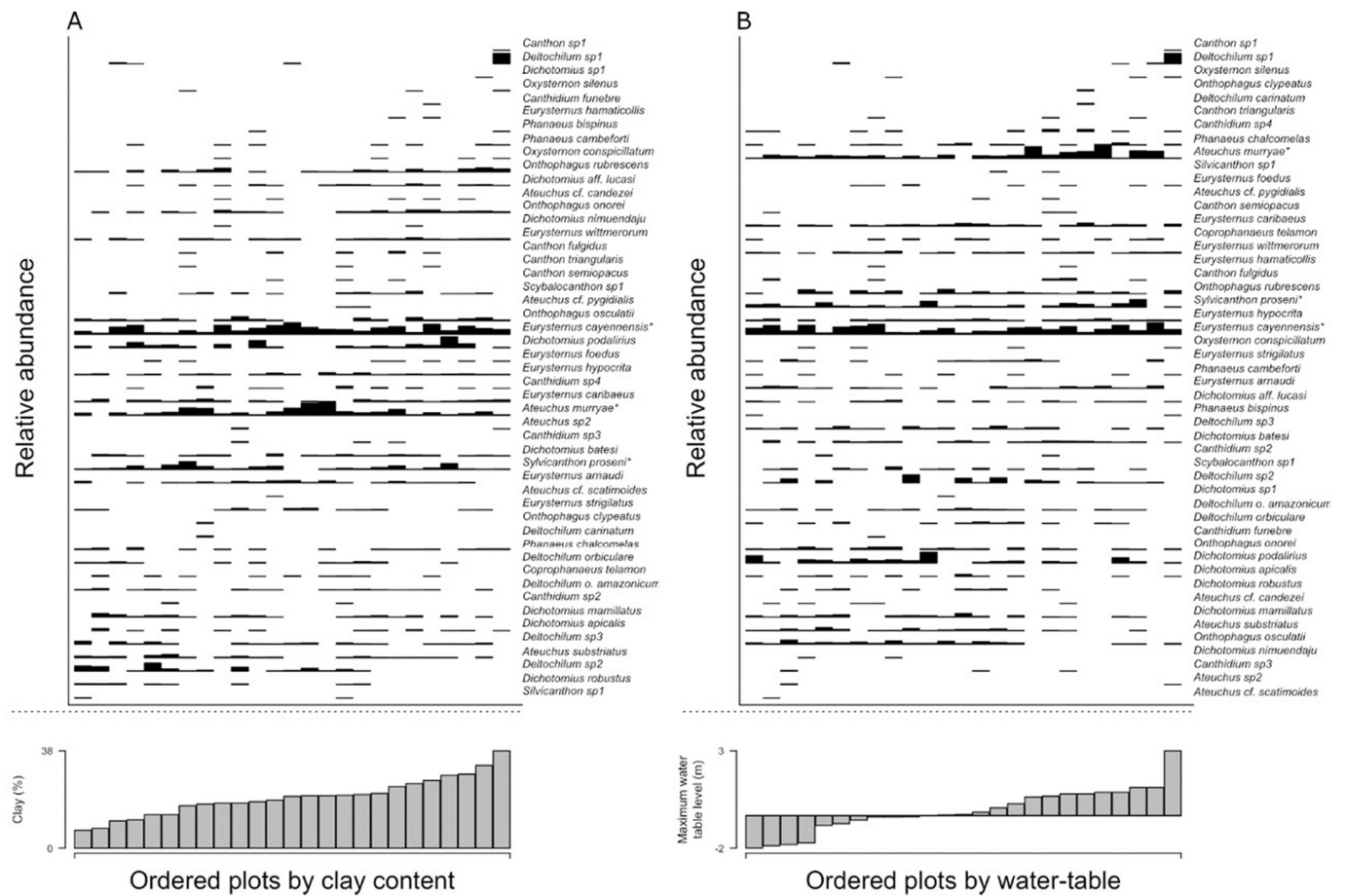


Fig. 3. Relative abundance of dung beetle species recorded in forest sites with distinct levels of clay content (A) and maximum water-table level (B) in 29 sampling sites on the BR319, northern interfluvium of Purus and Madeira rivers, Amazonia state, Brazil. Negative values of water table level indicate how far the water level is from the soil surface, while positive values represent the level of the water table above the soil surface. Asterisks in A and B indicate the dominant species.

Table 3
Summary statistics of *manyglm* function for the species composition of dung beetles in relation to predictor variables. *P*-values were based on 999 bootstrap permutations of residuals. Significant results are in bold.

Dependent variable	Predictor	LTR	Wald value	<i>P</i> -value
All assemblage		19.12		0.012
	Clay		10.070	0.006
	Silt		9.122	0.022
	Water-table maximum level		8.515	0.038
Dwellers		7.581		0.247
Rollers		12.83		0.001
Tunnellers	Clay		5.995	0.012
	Silt		3.145	0.588
	Water-table maximum level		3.803	0.419
	Clay	12.48	7.694	0.007
Silt		7.599	0.005	
Water-table maximum level		6.969	0.025	

podalirius, *S. proseni*) were spatially eurytopic. Although the three most abundant species were also the ones with widest spatial distributions, two of them (*A. murrayae* and *S. proseni*) were more abundant in specific soil conditions. Soil physical texture, together with water-table depth may affect habitat availability. Sandy soils may not sustain humid

conditions as long as clay soils, but clay soils may dry out and become extremely hard (Fincher, 1973; Osberg et al., 1994). Since beetles invest much time and energy in nesting activity (Brussaard and Slager, 1986; Sowig, 1996), they may be limited by soil conditions. Some dung beetle species that tolerate soils with contrasting physical conditions have plastic nesting strategies (e.g. Fincher, 1973; Sowig, 1996). For example, *Digitonthophagus gazella* digs shallower tunnels in compacted soils (Dabrowski et al., 2019). Nonetheless, nesting strategies in dung beetle species have behavioral limitations (e.g. depth of the burrows, number and length of brood chambers) and physical limitations (e.g. water-logged or highly compacted soils). Some dung beetle species only occur in specific soil conditions, as *Allogymnopleurus thalassinus*, which is restricted to soft sands, and *Allogymnopleurus consocius* that is restricted to areas with soft self-mulching clay (Osberg et al., 1994). Therefore, soil texture apparently is a limiting environmental condition for the dominant species of dung beetles in the Amazon region.

The diversity of soil associations may be related to the high diversification in Amazonia, allowing dung beetle species from the same feeding guild to specialize on different edaphic conditions (e.g. Larsen et al., 2006). According to our results, tunneller beetles showed a change in species composition depending on soil conditions. Such result suggests that tunnellers present broad environmental plasticity, with species adapted to dwell in sites with different soil properties. Nevertheless, there is still inconsistency regarding how soil conditions affect the diversity patterns of dung beetle functional groups (Farias and Hernández, 2017; Halffter and Edmonds, 1982; Silva et al., 2015). In our study, the effects of soil physical properties on the abundance of dung beetle functional groups may be biased by the most abundant species. For

example, the positive relation between dweller abundance and clay content may have been due to the trend in the dominant species in this group, *E. cayennensis*. The same may be likely for species composition trends observed herein. In our study, the trend of species composition (the significant effects of silt, clay and water-table level on species composition) observed in all dung beetle assemblage was similar to the one observed in the most speciose functional group (i.e. tunneller), but different from those observed among the roller and dweller beetles. Therefore, our results highlight that overall trend in ecological assemblages may depend on the relative weight (i.e. species richness, abundance) of each functional group.

The soil characteristics had subtle effects on dung beetle species richness. In our study, estimated tunneller species richness was higher in clay soils, suggesting that dung beetle species differ in their tolerance levels of the soil textural gradient. However, a tunneller dung beetle (*Phanaeus vindex*) may adapt to soil conditions, digging shallower tunnels when facing soils with higher amount of clay (Fincher, 1973). Besides, morphological traits of dung beetles are related to their interaction with the environment, and thus may favor or restrain beetle activity depending on habitat quality (e.g. soil type, vegetation structure, see Raine et al., 2018; Silva et al., 2015). Among different vegetation physiognomies, for example, semideciduous forests near Amazon forest supported larger tunneller and roller species compared to the fauna from submontane forests near Pantanal wetland (Silva et al., 2015). Therefore, it is possible that vegetation structure, not considered here, could also affect dung beetle diversity in our sampled area. Vegetation structure may have synergistic effects with soil properties, which may help explain the relative lower predictive power of soil properties on dung beetle species richness.

In one of the few studies of the effects of water-table properties on dung beetles, Brussaard (1985) showed that the length of tunnels constructed by *Typhaeus typhoeus* beetles may depend on water-table depth. In our study, the water-table maximum level was more related to species composition than species richness, considering all dung beetle species. In addition, water table affected roller beetles, which was started by the decrease in their abundance in sites with shallow water table. This is unanticipated, since only tunnellers were expected to be affected by water-table maximum level. In our study, nine species recorded in the sites with deepest water tables were absent at the sites with shallowest water tables. Sites with the shallowest water tables had five species that were not recorded at the sites with deepest water tables. The dung beetle species that changed in density along the water-table-maximum-level gradient were from different genera and functional groups (tunneller – *Dichotomius*, *Ateuchus*, *Canthidium*, *Coprophanaeus*, and *Oxysternon*; roller – *Canthon*, *Deltotilum*; dweller – *Eurysternus*). Several authors have posited that each functional group has a specific distribution in a niche space (Mason et al., 2005; Mouillot et al., 2012), and, to our knowledge, this study is the first showing how functional groups respond according to water table level. Previous studies focused on aboveground structure (e.g. vegetation structure, landscape parameters) as the most important drivers of dung beetle diversity in the tropics (Barreto et al., 2020; Cajaiba et al., 2018; Nichols et al., 2007). The results found here allow us to suggest that water table level also provides different ecological niches for dung beetle species, thus being an additional determinant of assemblage dynamics in tropical forests, especially those lying close to small streams. In the Amazon region, high water tables (<5 m depth) comprise one third of Amazon forests, and such forests are composed by vegetation that is resistant to droughts, which are considered potential refuges for biodiversity conservation (Sousa et al., 2020). Therefore, our results suggest that water-table maximum level may be an overlooked, but relevant, predictor that determines dung beetle species distribution in Amazon forests.

Despite the relatively well-known effects of landscape structure, habitat types, and microclimatic conditions on dung beetle diversity (Larsen et al., 2006; Nichols et al., 2007; Salomão et al., 2019), few studies have considered how soil properties affect dung beetle

assemblages (e.g. Brussaard, 1985; Davis, 1996a; Farias and Hernández, 2017; Silva et al., 2015). Our results suggest that soil texture and water table levels together determine the distributions of most dung beetles in shallow water table forests of central Amazonia, both within and among functional groups. Considering the Anthropocene scenario (Dirzo et al., 2014), it would be interesting to assess the resilience patterns of ecological communities facing anthropogenic landscape transformation. Therefore, future studies should focus on understanding the sensitivity of the assemblages to changes in the water table level regimes.

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.

Acknowledgements

RPS was supported by Programa Nacional de Pós-doutorado/Capes (Government funds PNPd/CAPES, Brazil). DAP received a master scholarship from FAPEAM. The collect of dung beetle was supported by the (FAPEAM) under grants conceded to APL (FAPEAM/CNPq/PRONEX process 586/10, Edital 003/2009-number 137). Water table level and soil data collection was supported by PRONEX-FAPEAM (1600/2006), Hidroveg Universal CNPq (473308/2009-6), FAPESP/FAPEM (465/2010). Modules infrastructure was installed by PPBio Manaus (CNPq 558318/2009-6) and INCT CENBAM (FAPEAM/FDB/INPA n° 003/2012 - Projeto INCT CENBAM Centro de Biodiversidade Amazônica). FBB is continuous supported by a CNPq grant (309600/2017-0 and 313986/2020-7), and JS by the CNPq grant 09/2020-PQ (314149/2020-1). Authors thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the continuous support, Dorival Cruz da Silva for monitoring the water table level in the field, and Thaise Emilio for obtaining the environmental variables.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.apsoil.2021.104260>.

References

- Akaike, H., 1982. On the fallacy of the likelihood principle. *Stat. Probabil. Lett.* 1, 75–78. [https://doi.org/10.1016/0167-7152\(82\)90019-0](https://doi.org/10.1016/0167-7152(82)90019-0).
- Arellano, L., Farías, P.M., Barois, I., Torres-Rivera, J.A., Meza, E., 2018. La importancia de un suelo saludable. In: Halffter, G., Cruz, M., Huerta, C. (Eds.), *Ganadería Sustentable en el Golfo de México*. INECOL, México, Xalapa, pp. 75–105.
- Baccaro, F.B., Rocha, I.F., del Aguila, B.E., Schiatti, J., Emilio, T., Pinto, J.L.P.D.V., Lima, A.P., Magnusson, W.E., 2013. Changes in ground-dwelling ant functional diversity are correlated with water-table level in an Amazonian terra firme forest. *Biotropica* 45, 755–763. <https://doi.org/10.1111/btp.12055>.
- Barragán, F., Moreno, C., Escobar, F., Halffter, G., Navarrete, D., 2011. Negative impacts of human land use on dung beetle functional diversity. *PLoS One* 6, e17976. <https://doi.org/10.1371/journal.pone.0017976>.
- Barreto, J.W., Salomão, R.P., Iannuzzi, L., 2020. Diversity of dung beetles in three vegetation physiognomies of the Caatinga dry forest. *Int. J. Trop. Insect Sci.* 40, 385–392. <https://doi.org/10.1007/s42690-019-00089-4>.
- Benchimol, M., Peres, C.A., 2015. Edge-mediated compositional and functional decay of tree assemblages in amazonian forest islands after 26 years of isolation. *J. Ecol.* 103, 408–420. <https://doi.org/10.1111/1365-2745.12371>.
- Blanchart, E., Albrecht, A., Bernoux, M., Brauman, A., Chotte, J.L., Feller, C., Ganry, F., Hien, E., Manlay, R., Masse, D., Sall, S., Villenave, C., 2007. Organic matter and biofunctioning in tropical sandy soils and implications for its management. In: *Management of tropical sandy soils for sustainable agriculture: a holistic approach for sustainable development of problem soils in the tropics*. Proceedings of the International Congress on Management of Tropical Sandy Soils for Sustainable Agriculture, Thailand, Khon Kaen, pp. 224–241.
- BRASIL, 1974. Projeto RADAM Folha SB20 Purus. O Projeto, Rio de Janeiro.
- Brussaard, L., 1985. A pedobiological study on the dung beetle *typhaeus typhoeus* (Coleoptera, Geotrupidae). University of Wageningen, Wageningen.
- Brussaard, L., Slager, S., 1986. The influence of soil bulk density and soil moisture on the habitat selection of the dung beetle *typhaeus typhoeus* in the Netherlands. *Biol. Fertil. Soils* 51–58. <https://doi.org/10.1007/BF00638961>.

- Cajaiba, R.L., Périco, E., Dalzochio, M.S., Silva, W.B., Bastos, R., Cabral, J.A., Santos, M., 2017. Does the composition of scarabaeidae (Coleoptera) communities reflect the extent of land use changes in the Brazilian Amazon? *Ecol. Ind.* 74, 285–294. <https://doi.org/10.1016/j.ecolind.2016.11.018>.
- Cajaiba, R.L., Périco, E., Silva, W.B., Leote, P., Santos, M., 2018. Are Small Dung Beetles (Aphodiinae) useful for monitoring neotropical forests' ecological status? Lessons from a preliminary case study in the Brazilian Amazon. *For. Ecol. Manag.* 429, 115–123. <https://doi.org/10.1016/j.foreco.2018.07.005>.
- Dabrowski, J., Venter, G., Truter, W.F., Scholtz, C.H., 2019. Dung beetles can tunnel into highly compacted soils from reclaimed mined sites in eMalaheni, South Africa, 134, 116–119. <https://doi.org/10.1016/j.apsoil.2018.10.015>.
- Davis, A.L.V., 1996a. Community organization of dung beetles (Coleoptera: Scarabaeidae): differences in body size and functional group structure between habitats. *Afr. J. Ecol.* 34, 258–275. <https://doi.org/10.1111/j.1365-2028.1996.tb00621.x>.
- Davis, A.L.V., 1996b. Habitat associations in a south african, summer rainfall, dung beetle community (Coleoptera: scarabaeidae, aphodiidae, staphylinidae, histeridae, Hydrophilidae). *Pedobiologia* 40, 260–280.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the anthropocene. *Science* 345, 401–406. <https://doi.org/10.1126/science.1251817>.
- do Amaral Pereira, L.G., Capavede, U.D., Tavares, V.C., Magnusson, W.E., Bobrowiec, P. E.D., Baccaro, F.B., 2019. From a bat's perspective, protected riparian areas should be wider than defined by Brazilian laws. *J. Environ. Manage.* 232, 37–44. <https://doi.org/10.1016/j.jenvman.2018.11.033>.
- Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M., Wilson, R., 2007. Dorman methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30, 609–628. <https://doi.org/10.1111/j.2007.0906-7590.05171.x>.
- Doube, B.M., 1990. A functional classification for analysis of the structure of dung beetle assemblages. *Ecol. Entomol.* 15, 371–383. <https://doi.org/10.1111/j.1365-2311.1990.tb00820.x>.
- Drucker, D.P., Costa, F.R.C., Magnusson, W.E., 2008. How wide is the riparian zone of small streams in tropical forests? A test with terrestrial herbs. *J. Trop. Ecol.* 24, 65–74. <https://doi.org/10.1017/S0266467407004701>.
- Fariás, P.M., Hernández, M.L.M., 2017. Dung beetles associated with agroecosystems of southern Brazil: relationship with soil properties. *Rev. Bras. Cienc. Solo* 41, e0160248. <https://doi.org/10.1590/18069657rbcs20160248>.
- Fariás, P.M., Arellano, L., Hernández, M.L.M., Ortiz, S.L., 2015. Response of the copro necrophagous beetle (Coleoptera: Scarabaeinae) assemblage to a range of soil characteristics and livestock management in a tropical landscape. *J. Insect Conserv.* 19, 947–960. <https://doi.org/10.1007/s10841-015-9812-3>.
- Favila, M.E., Halffter, G., 1997. The use of indicator groups for measuring biodiversity as related to community structure and function. *Acta Zool. Mex.* 72, 1–25.
- Fearnside, P.M., Graça, P.M.L.A., 2006. BR-319: Brazil's Manaus-Porto Velho highway and the potential impact of linking the arc of deforestation to Central Amazonia. *Environ. Manag.* 38, 705–716. <https://doi.org/10.1007/s00267-005-0295-y>.
- Filgueiras, B.K.C., Liberal, C.N., Aguiar, C.D.M., Hernández, M.L.M., 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. <https://doi.org/10.1590/S0085-56262009000300017>.
- Filgueiras, B.K.C., Iannuzzi, L., Leal, I.R., 2011. Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest. *Biol. Conserv.* 144, 362–369. <https://doi.org/10.1016/j.biocon.2010.09.013>.
- Fincher, G.T., 1973. Nidification and reproduction of *phanaeus* spp. in three textural classes of soil (Coleoptera: Scarabaeidae). *Coleopt. Bull.* 27, 33–37.
- Gardner, T.A., Hernández, M.L.M., Barlow, J., Peres, C.A., 2008a. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. *J. Appl. Ecol.* 45, 883–893. <https://doi.org/10.1111/j.1365-2664.2008.01454.x>.
- Gardner, T.A., Barlow, J., Araújo, I.S., et al., 2008b. The cost-effectiveness of biodiversity surveys in tropical forests. *Ecol. Lett.* 11, 139–150. <https://doi.org/10.1111/j.1461-0248.2007.01133.x>.
- Gotelli, N.J., Colwell, R.K., 2011. Estimating species richness. In: Magurran, A.E., McGill, B.J. (Eds.), *Frontiers in Measuring Biodiversity*. Oxford University Press, USA, New York, pp. 39–54.
- Halffter, G., Edmonds, W.D., 1982. The nesting behavior of dung beetles (Scarabaeinae): an ecological and evolutive approach. Instituto de Ecología, México DF.
- Hanski, I., Cambefort, Y., 1991. The dung beetle ecology. Princeton University Press, Princeton.
- Hanski, I., Koskela, H., 1977. Niche relations among dung-inhabiting beetles. *Oecologia* 8, 203–231. <https://doi.org/10.1007/BF00751601>.
- Hayashi, M., Rosenberry, D.O., 2002. Effects of ground water exchange on the hydrology and ecology of surface water. *Ground Water* 40, 309–316. <https://doi.org/10.1111/j.1745-6584.2002.tb02659.x>.
- Huerta, E., van-der-Wall, H., 2012. Soil macroinvertebrates' abundance and diversity in home gardens in Tabasco, Mexico, vary with soil texture, organic matter and vegetation cover. *Eur. J. Soil Biol.* 50, 68–75. <https://doi.org/10.1016/j.ejsobi.2011.12.007>.
- Iannuzzi, L., Salomão, R.P., Costa, F.C., Liberal, C.N., 2016. Environmental patterns and daily activity of dung beetles (Coleoptera: Scarabaeidae) in the Atlantic rainforest of Brazil. *Entomotropica* 31, 196–207.
- Jay-Robert, P., Errouissi, F., Lumaret, J.P., 2008. Temporal coexistence of dung-dweller and soil-digger dung beetles (Coleoptera, Scarabaeoidea) in contrasting Mediterranean habitats. *Bull. Entom. Res.* 98, 303–316. <https://doi.org/10.1017/S0007485307005615>.
- Junk, W.J., Piedade, M.T.F., Schöngart, J., Cohn-Haft, M., Adeney, J.M., Wittmann, F., 2011. A classification of major naturally-occurring amazonian lowland wetlands. *Wetlands* 31, 623–640. <https://doi.org/10.1007/s13157-011-0190-7>.
- Larsen, T.H., Lopera, A., Forsyth, A., 2006. Extreme trophic and habitat specialization by peruvian dung beetles (Coleoptera: scarabaeidae: Scarabaeinae). *Coleopt. Bull.* 60, 315–324. [https://doi.org/10.1649/0010-065X\(2006\)60\[315:ETAHSB\]2.0.CO;2](https://doi.org/10.1649/0010-065X(2006)60[315:ETAHSB]2.0.CO;2).
- Li, W., Chen, H., Yan, Z., Yang, G., Rui, J., Wu, N., He, Y., 2020. Variation in the soil prokaryotic community under simulated warming and rainfall reduction in different water table peatlands of the Zoige plateau. *Front. Microbiol.* 11, 343. <https://doi.org/10.3389/fmicb.2020.00343>.
- Magnusson, W.E., Lima, A.P., Luizão, R., Luizão, F., Costa, F.R.C., Castilho, C.V., Kinupp, V., 2005. RAPELD: a modification of the gentry method for biodiversity surveys in long-term ecological research sites. *Biota Neotrop.* 5, 19–24. <https://doi.org/10.1590/S1676-06032005000300002>.
- Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111, 112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>.
- Moran, D.L.E., Mauseel, P., 2002. Linking amazonian secondary succession forest growth to soil properties. *Land Degrad. Develop.* 13, 331–343. <https://doi.org/10.1002/ldr.516>.
- Mouillot, D., Grahon, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2012. A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* 28, 167–177. <https://doi.org/10.1016/j.tree.2012.10.004>.
- Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* 4, 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>.
- Nichols, E., Larsen, T., Spector, S., Davis, A.L., Escobar, F., Favila, M., Vulinec, K., 2007. Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. *Biol. Conserv.* 137, 1–19. <https://doi.org/10.1016/j.biocon.2007.01.023>.
- Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezcua, S., Favila, M.E., 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biol. Conserv.* 141, 1461–1474. <https://doi.org/10.1016/j.biocon.2008.04.011>.
- Nunes, C.A., Braga, R.F., Figueira, J.E.C., Neves, F.S., Fernandes, G.W., 2016. Dung beetles along a tropical altitudinal gradient: environmental filtering on taxonomic and functional diversity. *PLoS One* 11, e0157442. <https://doi.org/10.1371/journal.pone.0157442>.
- Osberg, D.C., Doube, B.M., Hanrahan, A., 1994. Habitat specificity in african dung beetles: the effect of soil type on the survival of dung beetle immatures (Coleoptera Scarabaeidae). *Trop. Zool.* 7, 1–10. <https://doi.org/10.1080/03946975.1994.10539236>. <https://doi.org/10.1080/03946975.1994.10539236>.
- Powers, J.S., Beknell, J.M., Irving, J., Pérez-Aviles, D., 2009. Diversity and structure of regenerating tropical dry forests in Costa Rica: geographic patterns and environmental drivers. *Forest Ecol. Manag.* 258, 959–970. <https://doi.org/10.1016/j.foreco.2008.10.036>.
- PPBio, 2020. Análise granulométrica – Dispersão total. http://ppbio.inpa.gov.br/Port/inventarios/ducke/pterrestre/Analise_granulometrica.pdf. (Accessed 27 August 2020).
- R Core Development Team, 2015. R foundation for statistical computing, Vienna.
- Raine, E.H., Gray, C.L., Mann, D.J., Slade, E.M., 2018. Tropical dung beetle morphological traits predict functional traits and show intraspecific differences across land uses. *Ecol. Evol.* 8, 8686–8696. <https://doi.org/10.1002/ece3.4218>.
- Rennó, C.D., Nobre, A.D., Cuartas, L.A., Soares, J.V., Hodnett, M.G., Tomasella, J., Waterlot, M.J., 2008. HAND, a new terrain descriptor using SRTM-DEM: mapping terra-firme rainforest environments in Amazonia. *Proc. SPIE* 112, 3469–3481. <https://doi.org/10.1016/j.rse.2008.03.018>.
- Salomão, R.P., Alvarado, F., Baena-Díaz, F., Favila, M.E., Iannuzzi, L., Liberal, C.N., Santos, B.A., Vaz-de-Mello, F.Z., González-Tokman, D., 2019. Urbanization effects on dung beetle assemblages in a tropical city. *Ecol. Ind.* 103, 665–675. <https://doi.org/10.1016/j.ecolind.2019.04.045>.
- Santos, E.A., Medeiros, M.B., Ferreira, E.J.L., Simon, M.F., Oliveira, W.L., Costa, F.R.C., 2020. Palm distribution patterns in the southwestern Brazilian Amazon: impact of a large hydroelectric dam. *Ecol. Ind.* 463, 118032. <https://doi.org/10.1016/j.foreco.2020.118032>.
- Schiatti, J., Emilio, T., Rennó, C.D., Drucker, D.P., Costa, F.R.C., Nogueira, A., Baccaro, F.B., Figueiredo, F., Castilho, C.V., Kinupp, V., Guillaumet, J., Garcia, A.R. M., Lima, A.P., Magnusson, W.E., 2014. Vertical distance from drainage drives floristic composition changes in an amazonian rainforest. *Plant Ecol. Div.* 7, 241–253. <https://doi.org/10.1080/17550874.2013.783642>.
- Schiatti, J., Martins, D., Emilio, T., Souza, P.F., Levis, C., Baccaro, F.B., et al., 2016. Forest structure along a 600 km transect of natural disturbances and seasonality gradients in Central-Southern Amazonia. *J. Ecol.* 104, 1335–1346. <https://doi.org/10.1111/1365-2745.12596>.
- Scholtz, C.H., Davis, A.L.V., Kryger, U., 2009. *Evolutionary biology and conservation of dung beetles*. Pensoft Publishers, Sofia.
- Silva, R.J., Ribeiro, H.V., Souza, M.F., Vaz-de-Mello, F.Z., 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, 31, 601–612.
- Silva, T.R., Medeiros, M.B., Noronha, S.E., Pinto, J.R.R., 2017. Species distribution models of rare tree species as an evaluation tool for synergistic human impacts in the Amazon rainforest. *Rev. Bras. Botânica* 40, 963–971. <https://doi.org/10.1007/s40415-017-0413-0>.

- Sombroek, W., 2000. Amazon landforms and soils in relation to biological diversity. *Acta Amazon.* 30, 81–100. <https://doi.org/10.1590/1809-43922000301100>.
- Sombroek, W., 2001. Spatial and temporal patterns of Amazon rainfall. *Ambio* 30, 388–396. <https://doi.org/10.1579/0044-7447-30.7.388>.
- Sousa, T.R., Schiatti, J., Souza, F.C., Esquivel-Muelbert, A., Ribeiro, I.O., Emílio, T., Pequeno, P.A.C.L., Philips, O., Costa, F.R.C., 2020. Palms and trees resist extreme drought in Amazon forests with shallow water tables. *J. Ecol.* 108, 2070–2082. <https://doi.org/10.1111/1365-2745.13377>.
- de Souza Holanda, P.M., de Souza, J.L.P., Baccaro, F.B., 2020. Seasonal fluctuation of groundwater level influences local litter-dwelling ant richness, composition, and colonization in the Amazon rainforest. *Ecol. Entomol.* 46, 220–231. <https://doi.org/10.1111/een.12954>.
- Sowig, T., 1996. Brood care in the dung beetle *Onthophagus vacca* (Coleoptera: Scarabaeidae): the effect of soil moisture on time budget, nest structure, and reproductive success. *Ecography* 19, 254–258. <https://doi.org/10.1111/j.1600-0587.1996.tb01252.x>.
- Vaz-de-Mello, F.Z., Edmonds, W.D., Ocampo, F.C., Schoolmeesters, P., 2011. A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Coleoptera: Scarabaeidae). *Zootaxa* 2854, 1–73. <https://doi.org/10.11646/zootaxa.2854.1.1>.
- Villa, P.M., Martins, S.V., Oliveira-Neto, S.N.O., Rodrigues, A.C., Safar, N.V.H., Monsanto, L.D., Gancio, N.M., Ali, A., 2018. Woody species diversity as an indicator of the forest recovery after shifting cultivation disturbance in the northern Amazon. *Ecol. Ind.* 95, 687–694. <https://doi.org/10.1016/j.ecolind.2018.08.005>.
- Wang, Y., Naumann, U., Wright, S.T., Warton, D.I., 2012. mvabund— an R package for model-based analysis of multivariate abundance data. *Methods Ecol. Evol.* 3, 471–474. <https://doi.org/10.1111/j.2041-210X.2012.00190.x>.
- Weltzin, J.F., Pastor, J., Harth, C., Brigham, S.D., Updegraff, K., Chapin, C.T., 2000. Response of bog and fen plant communities to warming and water-table manipulations. *Ecology* 81, 3464–3478. [https://doi.org/10.1890/0012-9658\(2000\)081\[3464:ROBAFP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[3464:ROBAFP]2.0.CO;2).