

Taxonomic and morphological diversity of the ground-dwelling ant fauna in Eastern Amazonian grasslands

Emely L.S. Siqueira^{a,b,*}, Rogério R. Silva^{b,**}

^a Programa de Pós-Graduação em Biodiversidade e Evolução - PPGBE, Museu Paraense Emílio Goeldi - MPEG, Belém, Pará, Brazil

^b Coordenação de Ciências da Terra e Ecologia, Museu Paraense Emílio Goeldi - MPEG, Av. Perimetral 1901, 66077-830, Belém, Pará, Brazil

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ABSTRACT

Amazonian grassland ecosystems are poorly understood, highly threatened, and under-protected. This study combined taxonomic and trait-based diversity approaches to provide the first description of the diversity of the ground-dwelling ant fauna of grasslands in Eastern Amazonia. We surveyed two types of open vegetation habitats: *campinarana* (unique to Amazonia; five sites) and savanna (two sites). Of the 89 ground-dwelling ant species we collected from pitfall traps, a few species were characteristic of open vegetation habitats. We found significant differences among these sites in terms of their species richness, which was positively associated with vegetation complexity. Morphological diversity, via species richness, was positively related to flooding and negatively related to soil cover. In conclusion, we observed some characteristic ant species of open vegetation habitats in Amazonian grasslands, and morphologically rich, ground-dwelling ant fauna. Further, a trait-based approach improved our understanding of community organization in the Amazon, which is the most bio-diverse tropical biome on Earth.

1. Introduction

The Amazon basin is heterogeneous, both in vegetation structure and composition, comprising a large number of local ecological units and a wide variety of phytophysiognomies (Ab'Saber, 2002). The dense ombrophilous forest (a type of rain forest) is the predominant phytophysiognomy in this basin, covering 53.63% of its surface area (Malhado et al., 2013). However, various types of grasslands also co-occur within these forests, forming ecosystems known as “savanna islands” or “Amazonian savannas”. The density of vegetation in these formations can vary widely, as some consist of poorly developed vegetation on exposed (sunlit) sandy soils, while others comprise dense formations that can sometimes be confused with forests, such as forested savanna and steppe-like forested savanna formations (IBGE, 2012; Ratnam et al., 2011). Each of these formations has distinct environmental characteristics from the others (i.e. luminosity levels, temperature and humidity conditions, and soil types) that influence its community structure (Tews et al., 2004).

The existence of various phytophysiognomies in the Amazon can be

explained by both the biotic and abiotic factors that have evolved in this region. Changes in the Earth's climate, combined with sedimentary and tectonic processes occurring during the Cenozoic Era (about 10.000 ya), were responsible for paleomorphological changes in the Amazon that, in turn, influenced the courses of rivers and systems of soil drainage in the region (Hoorn et al., 2010; Hoorn and Wesselingh, 2010; Rossetti et al., 2012). Currently, savanna islands occupy approximately 267,164 km² (about 5%) of the Amazonian territory, and almost 90% of these savanna islands are located in Bolivia and Brazil, with limited areas also present in Venezuela, Guyana, and Suriname (De Carvalho and Mustin, 2017). In the Brazilian Amazon, savanna islands are distributed mainly in the states of Amapá, Amazonas, Pará, and Roraima (Magnusson et al., 2008; Pires, 1973).

Most studies of the biodiversity of Amazonian grasslands have focused on vegetation, while only about 10% of such studies have focused on invertebrates (De Carvalho and Mustin, 2017). This represents an especially low percentage of studies considering that invertebrates represent more than 80% of the animal biomass in the tropics, and ants in particular constitute an estimated 25% of the animal

* Corresponding author. Coordenação de Ciências da Terra e Ecologia, Museu Paraense Emílio Goeldi - MPEG, Av. Perimetral 1901, 66077-830, Belém, Pará, Brazil.

** Corresponding author. Coordenação de Ciências da Terra e Ecologia, Museu Paraense Emílio Goeldi - MPEG, Av. Perimetral 1901, 66077-830, Belém, Pará, Brazil.

E-mail addresses: emelysiqueira@gmail.com (E.L.S. Siqueira), rogeriorosas@gmail.com (R.R. Silva).

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biomass in tropical forests (Fittkau and Klinge, 1973). De Carvalho and Mustin (2017) highlighted the potential for endemism in these ecosystems in Amazonia and the need for more information on how to conserve the biodiversity of savannas, which have been impacted by anthropogenic pressures in all parts of the world.

Ants have wide geographical distributions and occur in almost all terrestrial environments, and thus constitute one of the most diverse and well-adapted groups of invertebrates on Earth (Wilson and Hölldobler, 2005). Although the Amazon region is known to support the largest number of ant species on the planet, there have been few studies of the ant fauna of non-forested Amazon ecosystems (e.g., Souza et al., 2016; Vasconcelos et al., 2008; Vasconcelos and Vilhena, 2006), especially those of *campinarana* (Souza et al., 2016), a nutrient-poor, unique vegetation type in the Amazon biome that provides habitats to many endemic species of plants (IBGE, 2012).

Our understanding of ecological communities has significantly expanded with the use of trait-based approaches, which allow for an overview of how species composition is shaped by the environment, especially in hyper-diverse groups for which a large number of species are not known or have not been ecologically studied (Gibb and Parr, 2013; McGill et al., 2006; Wong et al., 2018). Studies of ant communities using trait-based approaches have shown that species' adaptive strategies in terms of their morphology, physiology, and behavior converge or diverge in similar and different environments, respectively, according to the biotic and abiotic characteristics of these environments (Schofield et al., 2016). For example, in more complex and interstitial environments, such as the leaf-litter of tropical forest floors, it is advantageous to have short legs for efficient locomotion between interstices, whereas in simpler and flatter environments, such as savannas, it is advantageous to have longer legs for agile locomotion aboveground (Gibb and Parr, 2013; Kaspari and Weiser, 1999; Weiser and Kaspari, 2006).

The effects of natural disturbances on invertebrate fauna in Amazonia open habitats have rarely been studied. In these habitats, ants can be exposed to the impact of seasonal flooding, which varies in strength and frequency. For example, the periodic flooding that characterizes *varzea* rainforests has an important imprint on leaf-litter ant communities, decreasing species richness by decrease nesting sites in comparison with *terra firme* forests (Adis and Junk, 2002), but low-disturbance habitats had similar species richness when differences in nest density is adjusted (Mertl et al., 2009). However, for open habitats in Amazonia, flooding varies with elevation, distance from rivers, heavy rainy periods, drainage restrictions or water-table elevation (IBGE, 2012), creating a large variation in disturbance onto which species and nest should respond.

In grassland areas, flooding immediately reduces the diversity, abundance and biomass of soil invertebrates, changing the structure of communities (Plum, 2005). This effect increases with flooding duration and increasing temperature. However, short and predictable floods, as those in the Amazonian savannas, can increase diversity by increasing abundance of opportunistic and generalist species of invertebrates. Flooding also support changes in morphological, phenological, physiological and behavioral (migration, temporal diving) traits, with numerous interactions among species (Adis and Junk, 2002; Plum, 2005).

In this study, we assessed the ant fauna inhabiting the open vegetation habitats of remote sites in the Eastern portion of the Brazilian Amazon. Our main aim was to describe these ant assemblages by combining taxonomic and morphological data to analyze the ant diversity in poorly studied, neglected, and highly threatened Amazonian grasslands. Herein, we assessed how local site characteristics influence the taxonomic and morphological diversity of ants. First, because species of ground-dwelling ants are associated with particular site characteristics (vegetation structure and abiotic factors), we expected to find higher taxonomic and morphological diversity in sites characterized by greater environmental complexity (i.e. taller vegetation and greater ground vegetation cover). Second, because seasonally flooded soils in

Amazon cause changes in the community structure of invertebrates, favoring the establishment of generalist species (Adis and Junk, 2002; Baccaro et al., 2013; Plum, 2005), we expected increased ground-dwelling ant diversity in open vegetation habitats in Amazonia experiencing temporary flooding disturbance.

2. Methods

2.1. Study area

We conducted our research in Portel, Pará, Brazil, a 25,384,960 km² municipality located in the Marajó mesoregion, north of Pará. The average total annual precipitation received by this region is 2349 mm, and there is a rainy season lasting from November to May and a dry season from June to October. The temperature is relatively constant throughout the year (annual average: 26.7 °C).

We selected sites for sampling by examining satellite images of the Marajó mesoregion (C = *Campinarana* site; S = Savanna site). We sampled seven locations: one site near Acuti Pereira River (Site C1), four sites near tributaries of the Camarapi River (Açaituba [C2], Mirituba [C3], and Banã [C4, C5]), and two sites near the hydrographic basin of Portel (Santa Rosa [S1] and Pacoval [S2]). All sites were located between 02°12'45"S, 50°30'48"W and 01°51'14"S, 50°37'55"W (Fig. 1).

The Marajó mesoregion comprises a variety of vegetation types, including lowland rainforest, dense alluvial forest, pioneer formations influenced by river and/or lake hydrologic regimes, non-forested formations (e.g., *campinarana* and savanna), and transitional zones between forested and non-forested formations. In this study, we focused on the Amazonian ant fauna inhabiting two main vegetation types: *campinarana* and savanna (Fig. 2). The *campinarana* vegetation type of the studied sites is classified as grassy-woody *campinarana*, in which poorly developed (short-statured) vegetation and sandy soil, occurred along the saturated floodplains of blackwater rivers and in isolated depressions in those floodplains. These *campinarana* areas are flooded during the rainy season, but become so dry at the peak of the dry season that they frequently burn (IBGE, 2012). In contrast, the savanna vegetation type, characterized as savanna parkland, was found in poorly drained habitats, and was usually dominated by spaced woody shrubs and small trees (including palms), usually all of the same species at each site, with a groundcover dominated by forbs and graminoids. The poor drainage of savannas is due to their clayey soils (with low permeability), which cause them to flood during the rainy season (IBGE, 2012).

2.2. Sampling design

We sampled ants using pitfall traps placed along 21 transects. Each transect was comprised of 20 equidistant pitfall traps, placed every 25 m over 500 m (with three transects at each site). Five sites (C1–C5) were in *campinarana* areas and two sites (S1 and S2) were located in savanna areas. Transects in the same site were at least 500 m and up to 1 km apart. Ant traps consisted of 10-cm diameter plastic containers, partly filled with a mixture of water, detergent, and salt (preservative) and operated for one 48-h period for each transect. Sampling occurred from October 2015 to June 2016 in the rainy season, but site C1 was sampled in transition of dry to the rainy period (October 2015), and sites S1 and S2 were sampled in transition of rainy to the dry period (June 2016).

2.3. Ant identification

Ant specimens captured in 420 pitfall traps (21 transects × 20 pitfalls) were sorted and identified to species or to morphospecies. We pinned 2686 individuals as a reference collection for the ant fauna collected in the region. Baccaro et al. (2015) was used to identify ants to genus, while the following keys were used to identify ants to species: Gonçalves (1961), Kempf (1966), Kugler and Brown (1982), Longino (2003), Albuquerque and Brandão (2004), Wild (2005), Wild and

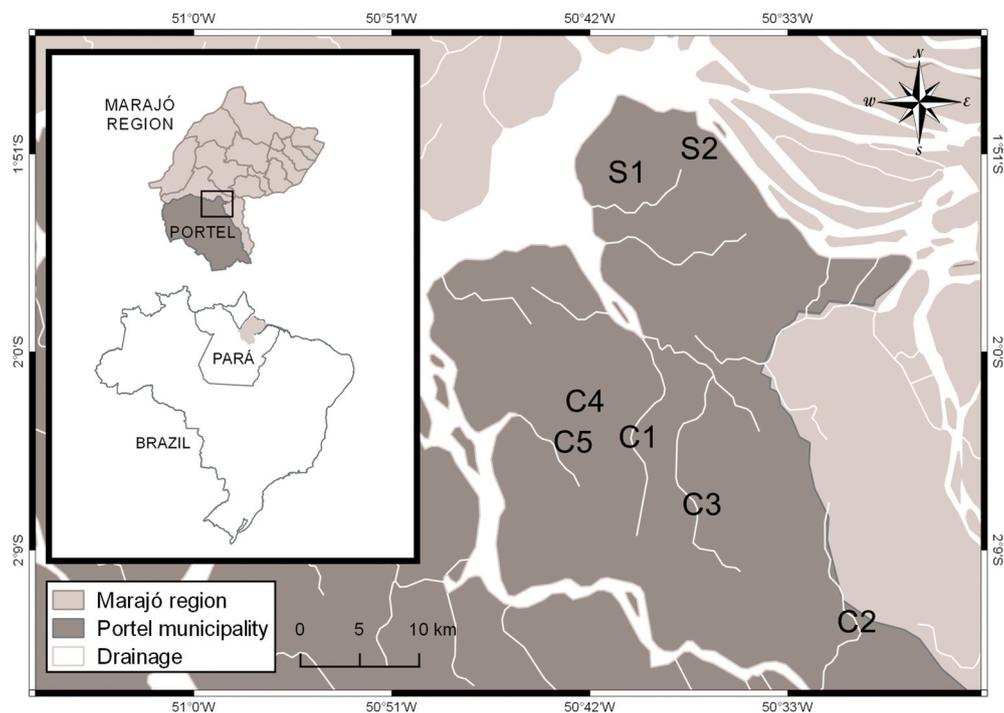


Fig. 1. Map showing the location of the study areas and the distribution of sampling sites in Portel municipality, Marajó region, state of Pará, Brazil. Abbreviations for *Campinarana*: C1 (Acuti Pereira), C2 (Açaituba), C3 (Mirituba), C4 (Banã I), C5 (Banã II), and for Savanna: S1 (Santa Rosa), S2 (Pacoval).

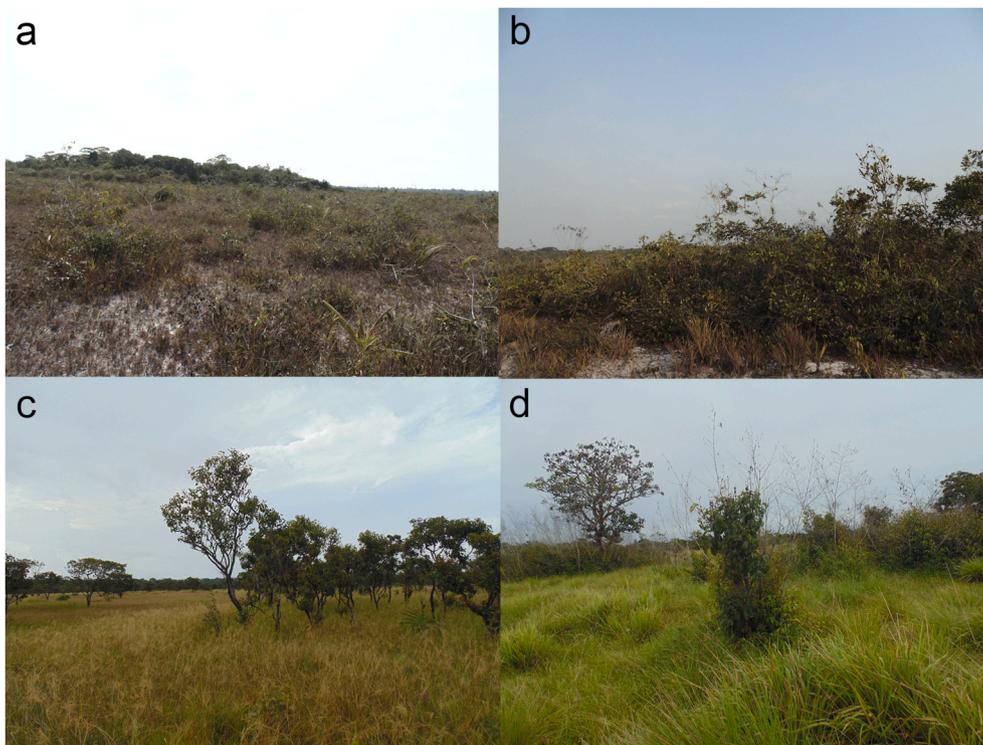


Fig. 2. View of a few grasslands studied in the Eastern Amazonia, Brazil. (a and b) *Campinarana*, characterized by low vegetation, arenaceous soils, heterogeneous landscape, and large areas of bare ground and (c and d) savanna, formed by shrubs and widely-spaced trees, groundcover of forbs and graminoids, with clayey or clay-sandy soils.

Cuezzo (2006), Lattke et al. (2007), MacKay and MacKay (2010), Lattke (2011), Ortiz and Fernández (2011), and Johnson (2015). We also compared our specimens to the ant collections of the Museu Paraense Emílio Goeldi (MPEG) and the Museu de Zoologia da Universidade de São Paulo (MZSP). In total, 40% of specimens were identified to species

(n = 35), while the remaining 60% were identified to morphospecies (n = 54). Voucher specimens were deposited in the entomological collection of the MPEG. Species abundances at the transect scale were based on the occurrence (presence/absence) of workers (occurrence in pitfall traps out of 20), rather than the total number of individuals (sensu

Bestelmeyer et al., 2000).

2.4. Morphological data

We examined sixteen morphological characters for each species that represented various aspects of ant ecology as follow: [1] Weber's length (WL) and [2] pronotum width (PrW) as proxies for body size, which is correlated with habitat complexity and metabolic functions (Gibb and Parr, 2013; Kaspari and Weiser, 1999; Weiser and Kaspari, 2006); head size as measured by [3] head length (HL) and [4] head width across the eyes (HW), which may vary allometrically to the body, being related to diet, since larger head accommodates larger and more stronger mandibular muscles, allowing capture of larger prey (Kaspari, 1993). Further, differences in size and shape of mandibles, estimated by [5] mandible length (ML) and [6] mandible width (MW), may reflect in dietary specialization, especially for predatory species (Weiser and Kaspari 2006); clypeus size, measured by [7] clypeus length (CL), may reflect diet mainly of species that use liquid foods (Davidson et al., 2004; Eisner, 1957); eye size, measured by [8] maximum length of the eye measured along its longer axis (EL), may indicate trophic level, mainly for predatory species, or may also characterize foraging period (diurnal or nocturnal) or microhabitat of nesting (Narendra et al., 2013; Weiser and Kaspari, 2006); eye position was estimated using [9] inter-ocular distance (ID) and the [10] distance of the eye from the mandible insertion (DEM). These combined measures can be used to determine eye position on head and since, the visual search performance for food and for orientation (Fowler et al., 1991; Weiser and Kaspari, 2006); antenna size, as estimated by [11] scape length (SL), is an important structure in mechanisms of chemoreception, influencing behavior and foraging, especially in species with reduced eyes (Weiser and Kaspari, 2006); leg size, as determined by [12] hind tibia length (TL) and [13] hind femur length (FL), may be allometric to body size and determines locomotion performance, which is related to habitat complexity (Gibb and Parr, 2010; Kaspari and Weiser, 1999).

Finally, we used petiole measurements, described by [14] petiole length (PeL), [15] petiole height (PeH), and [16] petiole width (PeW) as a body structure that impact directly ant fitness through its influence on workers and colony survival. Because petiole measures have not been precisely described in ant trait-based ecology, we following described the biological importance of the ant petiole.

We define petiole, connecting the mesosoma and gaster (where the sting apparatus is located or many types of chemical defenses), as a key trait in ant ecology, through interaction between ants and other organisms, between ants and the environment, ant predation or colony defense. Ants have the second abdominal segment strongly constricted into a distinct node-like petiole, forming a narrow waist between their mesosoma and gaster. Petiole takes the form of a node or of a scale of varying shape and size (Bolton, 1995; Hashimoto, 1996). Different groups of ants possess the waist formed by one or two nodes (the petiole and postpetiole, respectively). It may be a key trait in ant interaction or ant predation, considering the importance of the connection between mesosoma and gaster, where several exocrine glands and the sting apparatus (if present) are located. For example, in groups with a pedunculate petiole (i.e., longer petiole), the node is posterior and the petiole has higher mobility, presumably increasing power and flexibility of petiole-gaster articulation. Similarly, the flexibility of the gaster is increased by the additional constriction (post-petiole) (Hashimoto, 1996). Versatility of gaster movements should allow for better manipulation of prey or objects by workers (i.e., ant interactions with nest-mates, other organisms or even the substrate), which arguably contributed to the ants' ecological performance. Ant groups with post-petiole broadly attached to the gaster, may present a modification for increasing the length of tergal muscles (Hashimoto, 1996), presumably linked to trophic specialization (predation) as observed in Amblyoponinae and some Dorylinae. Note also that: (i) the types of musculature of petiole are associated with diverse functions on the

anterior abdominal segments (Hashimoto, 1996), (ii) ants show positional and functional modifications on the musculature of post-petiole which move the fourth abdominal segment; up- and downward movement of the gaster is also determined by muscles placed in petiole (Hashimoto, 1996); (iii) differences in waist structure of ants result in controlled telescopic and rotational movement at the IV abdominal segment, which facilitates abdominal mobility (Taylor, 1978). Additionally, petiole spines can have a defensive function in ants (Ito et al., 2016; Lenoir and Dejean, 1994), and petiole measures have been used to study morphological specialization in ants (Mertl and Traniello, 2009), changes in phenotypes of ant populations (Fedoseeva, 2011; Oliveira et al., 2015), and morphological organization of ant assemblages (Martello et al., 2018; Silva and Brandão, 2010, 2014). Finally, it's noteworthy that the fusion between the first abdominal and the third thoracic segments, with the subsequent appearance of the petiole, is widely considered a key evolutionary novelty that determined the success of the most diverse insect group in the world, the apocritan hymenopterans (Grimaldi and Engel, 2005).

We selected a large number of morphological characters because we were interested in obtaining a detailed description of the morphological space (hereinafter morphospace) of ants in grasslands, and also wanted to maintain consistency in our morphological datasets with those for ant assemblages throughout the remainder of the Neotropical region.

Measurements of pinned specimens (measurement error: ± 0.01 mm) were made using an ocular micrometer attached to a Zeiss Stemi SV 6 stereomicroscope. We used the highest magnification that allowed the measured trait to fit within the field of view. We measured traits in one to 16 specimens of each species (mean \pm standard deviation = 5 ± 3.43). Six individuals of each species were measured, when possible, which corresponded to the minimum replication currently adopted in studies of ant morphological diversity (Kaspari and Weiser, 1999; Parr et al., 2017; Silva and Brandão, 2010). There were 23 species represented by a single individual and ten species by two individuals in the morphological dataset.

We used Weber's length to indicate body size, and used the other attributes measured (of the head, mesosoma, metasoma, and body appendages) to indicate the specific shape of each ant. For polymorphic or dimorphic species, only measurements of minor-caste workers were included in the morphological data set. Trait measurements were standardized by Weber's length to decrease their strong correlations with body size ($r = 0.28\text{--}0.96$). We subsequently log-transformed mean trait values for all analyses, as is routinely done in trait-based studies of continuous morphological characters (Trisos et al., 2014).

2.5. Environmental data

We selected three variables to characterize the environments of the studied sites in terms of their habitat complexity and natural seasonal influences. We used 3 m \times 1 m plots to quantify the following habitat characteristics at the pitfall scale (i.e. at the scale of the 20 sampled points along each transect): (1) soil cover, which was estimated visually and described the percent vegetation cover of grasses, forbs, young shrubs, or palms rooted in the plot; and (2) the mean height of the vegetation in the plot, which was also estimated visually. At the transect scale, we also identified: (3) the presence (or absence) of traces of flooding. We defined flooding as either the presence of water in any part of the transects or signs that the soil was flooded before sampling in transects. We aggregated the environmental data measured at the pitfall trap-scale to the transect-scale (in each transect, as averaged values for soil cover and vegetation height and as frequency of occurrence for categorical variables).

2.6. Data analyses

All statistical analyses were carried out in the software R version 4.0.0 (R Core Team, 2020).

2.6.1. Ant taxonomic richness in open vegetation habitats in amazonia

Ant taxonomic richness was defined either as the observed species richness at the transect scale ($N = 21$) or at the site scale ($N = 7$). At the site scale, we estimated the number of species remaining to be sampled using the second-order Chao estimator (extrapolated species richness), based on the observed species richness. Sampling efficiency was then estimated as the number of species accumulated by trap sampling in each site relative to the total number estimated to be present within each assemblage. We inferred differences in estimated site richness using confidence intervals, where two groups are considered different when confidence intervals (95%) do not overlap. The species richness estimators associated with these estimates and confidence intervals were calculated using the "iNEXT" package (Chao et al., 2014; Hsieh et al., 2016).

2.6.2. The morphospace occupied by ant assemblages in open vegetation habitats in amazonia

We described the morphological structure of the ground-dwelling ant fauna in Amazonian grasslands based on a principal component analysis (PCA) performed on a correlation matrix of the 16 log-transformed variables measured for all 89 ant species collected. The PCA was computed using the "prcomp" function from the 'stats' package in R (R Core Team, 2020). The number of principal component axes retained was based on the broken-stick criterion, where a given axis may only be retained when its observed eigenvalues exceed the expected eigenvalues generated by the broken-stick model. We used the "bstick" function in the "vegan" package (Oksanen et al., 2011) to determine which axes to retain.

We defined morphological richness as the value of the trait richness using the TOP index or the trait onion peeling (sensu Fontana et al., 2015). The TOP index represents the sum of all successive areas touching all points in the trait distribution matrix. After the first minimum convex hull containing the outermost points has been built and its area has been measured, these points are deleted from the trait distribution and a second convex hull is calculated with the new outermost points. This process is continued until the number of remaining points is insufficient to create a convex hull. The sum of all the areas obtained in this way represents the TOP index (Fontana et al., 2015). Because the number of species found along transects must be higher than the number of traits (16 traits in our case) in this analysis, dimensionality reduction was required. We used as morphological traits the first six PCA axes representing 80% of variance in traits. These trait axes were standardized to have a mean of zero and unit variance (mean = 0; SD = 1), given standardization is important before calculating hull volumes and because of any a priori weighting on the ecological importance of the axes (Crouch and Ricklefs, 2019; Villéger et al., 2008).

We calculated standardized effect size (SES) for the TOP index values to remove any bias associated with differences in species richness among transects. SES values were calculated in null model analysis by dividing effect size (observed - expected [calculated from the mean of the null distribution]) by the standard deviation of the null distribution. We randomized the community matrix (21 transects, 89 species) using the "randomizeMatrix" function in the "picante" package (Kembel et al., 2010), while maintaining the observed species richness. We wrote our routine to calculate at the transect-scale the TOP index from 1999 simulated communities.

2.6.3. How local site characteristics determine the taxonomic and the morphological diversity of ants in open vegetation habitats in amazonia

We tested the effects of different environmental variables on the taxonomic and the morphological richness of ant assemblages using linear mixed models (LMEs) with a one-way random intercept model. The response variable was the observed richness and either the morphological richness or standardized morphological richness at the transect scale. We used vegetation structure (height), soil cover, and presence/absence of flooding as predictor variables in the models.

Further, observed richness was included in the two morphological diversity models to assess the influence of taxonomic species richness on morphological diversity. The site along the transect was included as the random term in the model. We used the "stepAIC" function with AICc to select the best model among all of those tested.

We calculated pseudo-R-squared for LME models using the "MuMIn" package (Barton, 2020), representing the variance explained by fixed factors (marginal R-squared). We assessed the overall variance explained by each predictor variable fitting two models. One model contained all predictors (the reference model), and the other model had one predictor dropped (Johnson, 2014).

3. Results

3.1. Ant taxonomic richness in open vegetation habitats in amazonia

In 420 pitfall traps, we noted 1653 occurrences of 89 ant species, representing 34 genera and seven subfamilies. Of these species, 63 were recorded in *campinarana* (27 unique species), and 62 in savanna (26 unique species).

Our study of the soil myrmecofauna of savanna and *campinarana* sites in the Marajó region revealed nine new species occurrences. We recorded *Pheidole scapulata* Santschi, 1923 and *Pheidole vallifica* Forel, 1901 for the first time in the Brazilian Amazon. Both species are associated with open areas (Wilson, 2003), suggesting that these ant species are specialized for open areas. We recorded two species not yet known for the state of Pará: (1) *Pheidole synarmata* Wilson (2003), which we collected in *campinarana*, although it is commonly found in litter-leaf in forests of Neotropical regions (Wilson, 2003); and (2) *Oxyepoecus vezeyii* (Forel, 1907), which we collected in savannas. This latter species has been found in Paraguay and Brazil and occurs in various ecosystems and biomes, but mainly in non-forested ecosystems. The present record is the first reported occurrence of this species in the State of Pará, as well as in Amazonian savannas. Further, we described five new species occurrences for the Marajó region: (1) *Acromyrmex balzani* (Emery, 1890) (registered in both *campinarana* and savanna sites); (2) *Gracilidris pombero* Wild and Cuzzo (2006) (registered in both *campinarana* and savanna sites); (3) *Centromyrmex brachycola* (Roger, 1861) (registered only in savanna sites); (4) *Pogonomyrmex naegelli* Emery, 1878, (registered only in savanna sites); and (5) *Strumigenys infidelis* Santschi, 1919 (registered only in savanna sites). With the exception of *C. brachycola*, these species are commonly collected in areas with dry vegetation types and nutrient-poor soils (Delabie et al., 2011; Johnson, 2015; Wild and Cuzzo, 2006).

The species richness observed per site ranged from 28 (in Mirituba) to 56 (in Pacoval), and the richness per transect ranged from 15 (in Acuti Pereira and Mirituba) to 39 (in Pacoval). The three transects with the highest species richness were all located in savanna sites. There were 32 unique species (those recorded in a single pitfall sample; range = 7–20 species per sample) and eight duplicates (species recorded in only two pitfall samples; range = 2–8 species per sample) (Table S.1). There was no difference in the extrapolated richness (Chao 2) between *campinarana* and savanna sites, although there were differences among sites, regardless of differences in their phytophysiology, based on the 95% confidence intervals of the Chao 2 index values (Table S.1, Fig. 3).

3.2. The morphospace occupied by ant assemblages in open vegetation habitats in amazonia

Based on the broken-stick criterion, two principal component (PC) axes were retained from the PCA ordination of the 16 morphological traits of the 89 species found, with 27.5% of the variation in morphological trait data being explained by PC1 (PCA Axis 1), and 19.5% explained by PC2 (PCA Axis 2) (Table 1, Fig. S.1). The coefficients of the eigenvectors for PC1 were negatively related to body size (WL = -0.344), eye position (ID = -0.166), and leg size (TL = -0.225, FL =

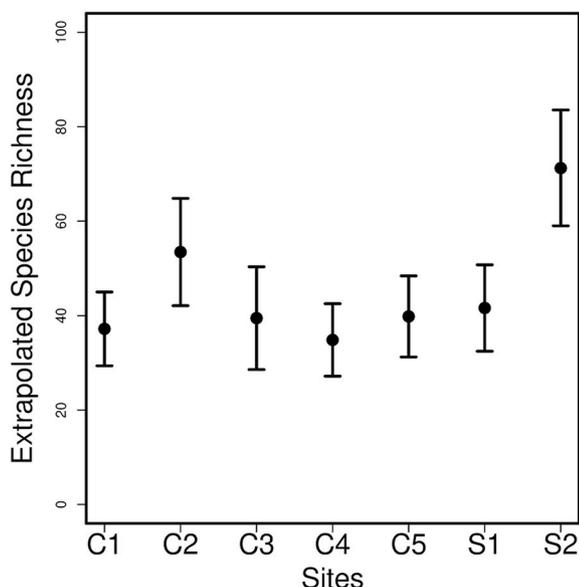


Fig. 3. Extrapolated species richness for ground-dwelling ant assemblages sampled in five *campinarana* and two savanna sites in Eastern Amazonia, Brazil, based on 60 pitfall traps in each site (20/transect). Chao 2 estimated species richness, with 95% confidence intervals. Abbreviations for *Campinarana*: C1 (Acuti Pereira), C2 (Açaituba), C3 (Mirituba), C4 (Banã I), C5 (Banã II), and for Savanna: S1 (Santa Rosa), S2 (Pacoval, Marajó, Pará, Brazil).

-0.141), and positively related to head size (HL = 0.396, HW = 0.400), eye length (EL = 0.378), pronotum width (PrW = 0.346), clypeus length (CL = 0.295), and mandible length (ML = 0.274). Therefore, PC1 described the allometry between body size and head size, eye size, clypeus size, and mandible size (Table 1, Table S.2, and Fig. S.2).

The coefficients of the eigenvectors for PC2 were negatively related to petiole size (PeL = -0.275, PeH = -0.162, PeW = -0.118) and positively related to scape length (SL = 0.466) and leg size (FL = 0.485, TL = 0.451). Therefore, species with highly positive values for PC2 tended to have large heads and long legs relative to their body size, while species with highly negative values for this PC tended to have

Table 1

Characteristics of principal component axes. Principal component analysis (PCA) was performed on correlation matrix of 16 ant traits and 89 ant species collected in five *campinaranas* and two savanna sites in Eastern Amazonia, Brazil. The four highest loadings on the first two principal components are highlighted in bold. Principal components were retained using a broken-stick model.

	PC1	PC2
Eigenvalue	4.396	3.117
Variance (%)	0.27	0.19
Cumulative variance (%)	0.27	0.47
Eigenvectors		
Weber's length (WL)	-0.344	0.104
Head width (HW)	0.400	0.157
Head length (HL)	0.396	0.130
Eye length (EL)	0.378	0.178
Inter-ocular distance (ID)	-0.166	0.264
Distance of the eye to the mandible insertion (DEM)	0.017	0.215
Scape length (SL)	-0.052	0.466
Clypeus length (CL)	0.295	0.184
Mandible length (ML)	0.274	0.012
Mandible width (MW)	-0.090	0.086
Pronotum width (PrW)	0.346	0.212
Hind tibia length (TL)	-0.225	0.451
Hind femur length (FL)	-0.141	0.485
Petiole length (PeL)	0.149	-0.275
Petiole height (PeH)	0.047	-0.162
Petiole width (PeW)	0.085	-0.118

large petioles relative to their body size (Table 1, Table S.2, and Fig. S.2).

3.3. How local site characteristics determine the taxonomic and the morphological diversity of ants in open vegetation habitats in amazonia

The best model for taxonomic diversity retained vegetation height as predictor variable (pseudo-R-squared = 0.19). Species richness tended to be higher along transects with taller vegetation (Fig. S.3, Table 2, and Table S.3). The best model for morphological diversity had species richness, soil cover, and presence of signs of flooding as predictors of morphological diversity (pseudo-R-squared = 0.77). Morphological diversity had higher values in flooded transects and had a negative association with soil cover at the transect scale (Table S.3; Fig. S.4). Species richness had the strongest positive relationship with morphological diversity, explaining most of variance captured by the model, followed by soil cover, and flooding (Table 2).

The standardized effect size for morphological diversity tended to be higher along transects with signs of flooding and tended to decrease with increasing soil cover (Table 2, Table S.3), representing morphological diversity higher and lower than expected, respectively. The pseudo-R-squared was lower, explaining 17% of overall variance, largely due to the absence of correlation between species richness and SES values.

4. Discussion

This study was the first to describe the ant fauna in *campinarana* habitats (a vegetation type unique to the Amazon), and the first to describe patterns in ant morphology in Amazonian grasslands. We sampled remote and never-before-studied open vegetation (i.e. non-forested) habitats. Our trait-based approach revealed environmental factors associated with ant morphological diversity. The diversity of ants (taxonomic or morphological) and environmental complexity (as measured by soil cover and vegetation height) were associated at the transect scale. Further, flooded transects showed greater diversity if ant

Table 2

Summary of fixed effect results in the linear mixed-effects models for taxonomic and morphological diversity of ground-dwelling ant fauna of grasslands in Eastern Amazonia. In the taxonomic diversity model, the fixed term included vegetation height, soil cover, and flooding as predictor variables. In the morphological diversity model (TOP index), the fixed term included species richness, vegetation height, soil cover, and flooding as predictor variables. In the morphological diversity model based on SES values, the fixed term included vegetation height, soil cover, and flooding as predictor variables. In all models, the random-term was site transect. Only the best models are described (determined by stepwise procedure with AICc). Marginal pseudo-R-squared represents the variance explained by fixed factors in the best model. AICc and the overall variance explained by each predictor variable represents AICc and marginal pseudo-R-squared if the model had the predictor dropped, respectively. Sobs = observed species richness at transect scale (N = 21); LTR = Likelihood ratio test; AICc = Second-order Akaike Information Criterion (AIC for small samples).

	Df	AICc	LRT	Pr (>Chi)	Marginal pseudo-R-squared
Taxonomic model: Sobs ~ Vegetation height					0.38
Intercept		134.66			
Vegetation height	1	134.90	3.33	0.0679	0.19
Morphological model: TOP index ~ Sobs + Soil cover + Flooding					0.77
Intercept		219.35			
Sobs	1	238.53	23.186	0.0001	0.25
Soil cover	1	220.82	5.479	0.0192	0.71
Flooding	1	219.78	4.437	0.0352	0.72
Morphological model: Standardized TOP index ~ Soil cover + Flooding					0.17
Intercept		70.75			
Soil cover	1	70.52	3.262	0.0709	0.05
Flooding	1	70.06	2.808	0.0937	0.02

traits were included in the model (i.e., an index of morphological diversity). Indeed, transects associated with flooding actually appeared to increase via species richness the morphological diversity of ground-dwelling ants in the studied Amazonian grasslands.

4.1. Ant taxonomic richness in open vegetation habitats in amazonia

We found a few significant differences in species richness, regardless of vegetation type (i.e. *campinarana* or savanna sites; Table S.3, Fig. 3). In general, sites with higher species richness corresponded to habitats with more complex vegetation (for example, greater soil cover and vegetation height). A relationship between habitat complexity and species richness in ant communities has previously been shown to exist in a wide range of environments (Pacheco and Vasconcelos, 2012; Stein et al., 2014; Stein and Krefl, 2015).

Among *campinarana* sites, we found higher species richness in habitats with higher densities of woody species, taller shrubs, and deeper leaf-litter. These results are similar with those of Franklin et al. (2005) in Amazon savannas where the distribution of mesofauna varied according to vegetation structure (shrubs and grasses), increasing in areas showing greater heterogeneity and wider range of niches. It is well known that the ant fauna is affected directly and indirectly by the structure of the vegetation (Vasconcelos et al., 2008). Based on this, we hypothesize that the habitat heterogeneity of *campinarana* and savanna sites in Amazonia may be responsible for the wide among-site variation we observed in ground-dwelling ant species richness.

4.2. The morphospace occupied by ant assemblages in open vegetation habitats in amazonia

The morphological organization of ant assemblages we described reflected the morphological characteristics of the ant fauna inhabiting relatively homogeneous environments, with medium to large-sized species, long legs for locomotion in open habitats, and large eyes positioned dorsally, which may allow better visual orientation and locomotion in the environment or improved performance of predators. However, upon closer examination some quite specialized attributes were found in this study among the ants occurring in the open vegetation habitats of Amazonia.

Tropical forests usually harbor very small ant species (miniaturized workers or dwarf workers) that have narrow heads (<1 mm), small bodies (<2 mm) (Peeters and Ito, 2015), and relatively small eyes (Salas-Lopez et al., 2017; Weiser and Kaspari, 2006). These morphological characteristics are advantageous for walking and foraging in leaf litter interstices (Kaspari and Weiser, 1999), and so favor certain resource acquisition strategies (e.g., thievery or the ability to dominate food resources) that may enable some species to attain high population densities (e.g., small-sized *Solenopsis* inhabiting leaf-litter; Delabie et al., 2000). The ant fauna inhabiting the studied grasslands did not include dwarf workers, which was probably related to the environmental characteristics of these habitats.

The ant communities in our study included few specialized predators or small-sized generalist predators. However, although we did not survey inquiline ant species in termite nests or subterranean species associated with soil layers and grass roots, we hypothesize that more inclusive surveys considering these microhabitats could significantly enrich the description of the morphospace occupied by ants in Amazonian grasslands. Our survey provides an opportunity to make more thorough comparisons of the morphospace occupied by ants in Amazonian grasslands with those of ants in others habitats in more complex ecosystems (e.g., *terra firme* forests).

4.3. How local site characteristics determine the taxonomic and morphological diversity of ants in open vegetation habitats in amazonia

We tested the relationship between local site characteristics and

either the taxonomic diversity or morphological diversity at transect scale. In our study, taxonomic richness was related to vegetation height in open vegetation habitats in Amazonia. Ground invertebrates increase in shrubby areas as they provide a deeper soil layer, improving water retention and reducing temperature at ground level (Athias, 1976; Franklin et al., 2005).

On the other hand, morphological diversity was higher in transects seasonally flooded, although this pattern was largely associated with species richness. It is well known that many ecological metrics depend on richness, such as measures of functional richness (Cornwell et al., 2006). For ants, a few studies have also described that overall functional diversity was significantly positively related to species richness (e.g., Arnan et al., 2015a), but environment may explain larger percentage of variation in functional diversity than in taxonomic diversity (Arnan et al., 2015b). Morphological diversity also increases with flooding for standardized values (against richness) but the variance explained by the model is comparatively lower. Therefore, the presence of seasonally flooded soils at a transect increased the diversity of the traits of its ground-dwelling ant fauna.

The effects of flooding on ant morphological diversity have not yet been studied, but if shallowly flooded savanna habitats contain a mixture of ant species found in both open habitats and deeply flooded habitats (Mertl et al., 2009), then the morphological diversity in such habitats could increase, as we reported in our study. Further, it has been shown that high water tables (flooded soils) in Central Amazonia forests may increase local alpha diversity by increasing the number of generalist species but decreasing the number of specialist predators and small hypogeic generalist foragers (Baccaro et al., 2013). Indeed, some specialist ant predators can be particularly intolerant to flooding (Mertl et al., 2009).

5. Concluding remarks

The Amazonian grasslands are ecosystems susceptible to seasonal flooding that may affect the maintenance of nesting ant species. For hyperdiverse groups such as ants, the use of combined taxonomic and morphological approaches can improve our understanding about flooding effects on ant assemblages, especially in open environments, where diversity is smaller if compared to forested ecosystems. We show that morphological traits help explain some of ant diversity and its answer to environments that suffered flooding. Furthermore, we have found in open vegetation habitats of Amazonia a morphological rich and poorly known ant fauna.

Author's contribution at the end of the manuscript

E.L.S.S. and R.R.S. conceived the experiment. E.L.S.S. carried out the experiment. R.R.S. analyzed the data. E.L.S.S. took the lead in writing the manuscript. Both, E.L.S.S. and R.R.S. authors contributed to the final version of the manuscript.

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Declaration of competing interest

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

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Appendix A. Supplementary data

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