


# Seasonal fluctuation of groundwater level influences local litter-dwelling ant richness, composition, and colonization in the Amazon rainforest

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**Abstract.** 1. Groundwater fluctuation follows the rainfall regime and is a natural source of disturbance by limiting the soil volume available for ant nesting. However, in areas with shallow water-table unpredicted floods are more frequent, which may also affect the distribution of litter ant species. Here, we evaluated the behavioural responses and diversity changes of litter-dwelling ants related to groundwater level fluctuation in the central Amazon tropical rainforest.

2. The natural occurrence of vertically stratified litter (above the ground level) accumulated at the base of stemless palms was a control sample in a series of paired samples. We used baits to measure ant activity and Winkler extractors to measure ant diversity in 10 riparian plots during the rainy (shallow water-table) and dry (deep water-table) season. We also added processed litter to count the number of new colonies found in both habitats.

3. We found fewer ant species and less occurrence during the rainy season. The assemblage composition was more heterogeneous during rainy season compared to same locations during dry season. However, ant activity such as recruitment and investment in resource monopolization showed an opposite pattern. The investments in reproduction followed ant recruitment to baits, with more colonies found in the leaf-litter during the dry season. All changes were strongly decreased or absent from the control locations.

4. Our results suggest that unpredicted floods mediated by water-table fluctuation may act as a disturbance to most ant litter species but may favour resource monopolization and litter colonization.

**Key words.** Disturbance, formicidae, tropical forests, water table.

## Introduction

Disturbances are common in nature; they are events that affect communities by influencing the availability of resources and space or by altering the physical environment (Seidl

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*et al.*, 2017). The direct effects of disturbances on biodiversity can be generally grouped in two main lines. The first is based on the idea of environmental template (Southwood, 1977) and predicts that frequent disturbances select more resilient species, often resulting in reduced biodiversity. The second line is based on several models on community structure such as the intermediate disturbance hypothesis (Connell, 1978; D'Amen *et al.*, 2017), the dynamic equilibrium model (Huston, 1979; Scholl & Wiens, 2016), and the patch dynamics model (Pickett & White, 1985). The first two models (Connell, 1978; Huston, 1979) are based on the hypothesis of community structuring by competition, according to which, under stable environmental conditions, intense biotic interactions forge

communities dominated by a few specialized species with highly competitive abilities. Periodic disturbances are supposed to reduce the growth of the dominant populations and allow the coexistence of other species. The intermediate disturbance hypothesis, based on the trade-off between colonization and competition capacity, argues that diversity tends to be higher in intermediate conditions of disturbance, where good colonizers and good competitors may be present (Connell, 1978; but see Fox, 2013 for a critical review about this hypothesis). The patch dynamics model (Pickett & White, 1985; Seidl *et al.*, 2017) is based on similar assumptions but adds that the disturbances produce habitat spots suitable for recolonization, which generates greater biodiversity at larger scales.

Ants are an ideal model to investigate hypotheses concerning the contribution of disturbance in structuring local assemblages. Ants are abundant in most ecosystems (Fittkau & Klinge, 1973; Ellwood & Foster, 2004), easily sampled (Agosti *et al.*, 2000), highly interactive (Stuble *et al.*, 2017), and have an extensive literature about competitive relationships (Cerdá *et al.*, 2013). In many assemblages, ant species follow a competitive hierarchy, where dominant species may affect the foraging (Fellers, 1987; Savolainen & Vepsäläinen, 1989; Arnan *et al.*, 2011; but see Parr & Gibb, 2012) and the foundation of new colonies of subdominant and subordinate species (Savolainen & Vepsäläinen, 1989; Philpott, 2010). However, the contribution of competitive interactions to assemblage structure is related to the sampling method employed (Ribas & Schoereder, 2002) and the spatial scale investigated (Baccaro *et al.*, 2012); therefore, competition alone may be insufficient to explain ant assemblage organization in many ecosystems (Andersen, 2008). Environmental disturbances such as fires, floods, or human activities can change the outcomes of ant assemblage hierarchies in different ways (Cerdá *et al.*, 2013). Depending on the biogeographical context, natural or anthropogenic disturbances may favour dominant or subdominant species (Andersen *et al.*, 2007; Stuble *et al.*, 2009) or disrupt the competitive hierarchy at the assemblage level (Arnan *et al.*, 2007; Sanders *et al.*, 2007).

Groundwater level may function as a natural source of disturbance for ant species that nest in the soil (Seal & Tschinkel, 2010; Tschinkel *et al.*, 2012). Areas with shallow water tables have limited soil volume in which ant colonies can nest, consequently affecting the spatial distribution of ant species (Seal & Tschinkel, 2010). During the rainy season in tropical forests, the shallow water table may saturate the soil favouring unpredicted floods especially after heavy rains (Baccaro *et al.*, 2013). Therefore, the disturbance mediated by the shallow water table may also extend to the ant litter-dwelling assemblage. The responses of disturbance caused by nest flooding are species-specific, with some species more responsive than others (Wilson, 1986; Adams *et al.*, 2011). For instance, the presence of generalist/dominant species is favoured in areas with shallow water tables and frequently flooded areas (Mertl *et al.*, 2009; Baccaro *et al.*, 2013). However, to what extent the increase in abundance of dominant species is the result of the colonization process or resistance to disturbance is still largely unknown.

The accumulated litter at the base of stemless palms may represent a more stable and relatively perennial place for the

establishment of ant colonies compared to the forest floor (Franken & Gasnier, 2010). Stemless palms are abundant in the Amazon forests (Henderson *et al.*, 1995) and are found from bottomlands to plateaus (Kahn & de Castro, 1985). Due to the arrangement of the leaves, the bases of stemless palms are funnel-shaped, within which often accumulates a thick and structurally complex layer of dead leaves and plant debris that have fallen from the trees above (Vasconcelos, 1990). These sites often have leaves and other plant materials at different stages of decomposition (Ribeiro *et al.*, 1995) and are often colonized by ants (Vasconcelos, 1990; Franken *et al.*, 2013). The accumulated litter at the base of stemless palms are above ground level; therefore, these sites do not suffer the direct effect of water table fluctuations and unpredicted floods and may represent important stable nesting sites for ants and other arthropods that live in leaf litter. In this case, the accumulated litter at the base of stemless palms would be more stable over the water table cycle, functioning as dispersal centres for frequently disturbed sites.

We evaluated the role of disturbance caused by groundwater level fluctuation on the structure and colonization process of ground/litter ant assemblages. More precisely, we hypothesized that natural disturbances mediated by water table fluctuations affect ant assemblage composition; more ant species, greater occurrence, and greater dominance will be found during the dry season (deeper water-table periods) on leaf-litter. We further hypothesized that the same diversity predictors have little variance along water-table periods in leaf-litter accumulated at the base of stemless palms. Water table fluctuation is synchronized with ant colonization process; therefore, more colonies are found in stable sites (base of stemless palms) and during the dry season (deeper water-table periods).

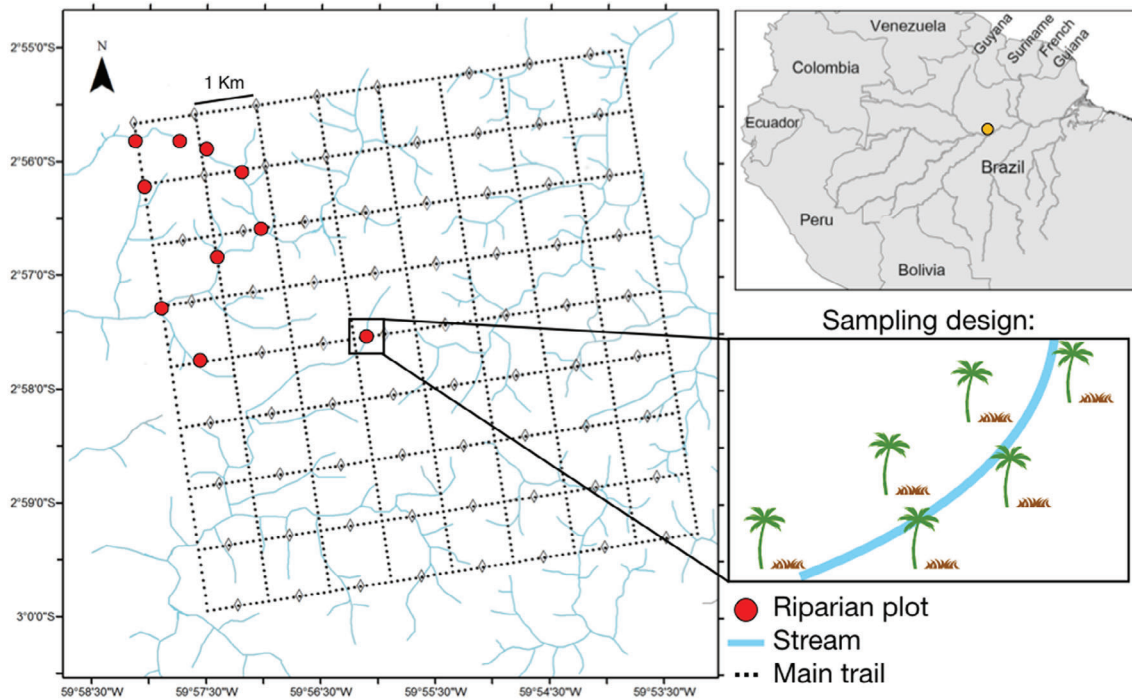
## Materials and methods

### Study area

The study was conducted in the Ducke Reserve at AM-010 highway, Km 26, Manaus, Amazonas, Brazil (3°05'S, 60°00'W) (Fig. 1). The reserve was established in 1963 and belongs to the National Institute of Amazonian Research (INPA) with a total area of approximately 100 km<sup>2</sup>. The relief is moderately undulated, with an altitudinal range of approximately 80 m between plateau tops and bottomlands. Within the reserve, there are three major habitat types: (1) plateau forest, located in the highest and flattest areas with well-drained clay soils, (2) bottomland forests or valleys, located in lower areas and near to streams with sandy and wet soils, and (3) slope forests, occurring on the slopes of the plateaus to the bottomlands (Hopkins, 2005; Oliveira *et al.*, 2009). The average annual rainfall in the Ducke Reserve is ~2400 mm. March and April normally have the highest rainfall (rainy season) and August and September are the months with least rainfall (dry season) (Marques Filho *et al.*, 1981).

### Sampling design

We sampled 10 bottomland riparian plots maintained by the Research Biodiversity Program (PPBio). The PPBio riparian



**Fig. 1.** Ducke Reserve north of Manaus city, Amazonas State, Brazil. Red points represent the riparian plots studied. The inset shows a schematic representation of the paired-sample design. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

plots are transects of 250 m in length adjacent to streams (Magnusson *et al.*, 2013). The 10 plots were sampled during March 2014 (rainy season – shallow water table) and September 2015 (dry season – deeper water table). The distance between plots ranged between 350 m and 3.5 km (Fig. 1). All plots were adjacent to small streams, which minimised variation in the water table level within plots. The riparian plots may be temporarily (1–2 h) flooded, or have intermittent ponds after heavy rains due to stream overflowing, especially during the rainy season (Espírito-Santo & Zuanon, 2017).

#### Sampling leaf-litter ants

In each plot, six stemless palms *Attalea microcarpa* Mart. (Arecaceae) were marked and the litter trapped in their bases, hereafter litter of stemless palms, were collected (Appendix S1). At the same time, six samples from the area adjacent to the stemless palms, hereafter leaf litter, were also sampled (Fig. 1), resulting in 120 samples during the rainy season and 120 samples during the dry season. The choice of sampling points within the plot was determined by the presence of stemless palms, but an attempt was made to distribute sample pairs ~25 m apart along the plot. The sampled stemless palms and leaf litter areas were marked with plastic tape to prevent the same palm tree and leaf litter area being resampled during the subsequent field campaign.

All litter of stemless palms was removed; the volume was rapidly measured using a graduated bucket and transferred to a Winkler sifter. The volume of leaf litter from the forest floor was

standardized by the volume sampled in the adjacent stemless palm and transferred to a Winkler sifter. Therefore, the overall volume of leaf litter sampled in the stemless palm bases and the adjacent area was similar in each plot. In the rainy season, litter sampling only occurred at least 3 h after heavy rain. The litter sifting time in the Winkler sifter was standardized to 1 min. The sifted litter was transported in cloth bags to the mini-Winkler extractors installed in the Ducke Reserve laboratory. In the laboratory, the mini-Winkler extractors were hung, and sieved litter was placed in 1 cm diameter nets and individually placed inside the mini-Winkler bags. The litter sample was held within a mini-Winkler bag for 48 h to extract the ants present in the litter (Delsinne & Arias-Penna, 2012).

The litter trapped in the stemless palms are more vertically structured, with humus-like litter in the bottom, compared with the top (Franken *et al.*, 2013). This vertical structure is not present in the leaf litter. However, this difference in litter structure is directly connected with your hypothesis. Given that the vertical layering in the litter trapped in stemless palms decreases the impact of unpredictable flooding, the litter of stemless palms is a more stable habitat over time.

#### Quantification of ant species dominance

The dominance relationships in ant assemblages can be evaluated in different ways (Parr & Gibb, 2010). In this study, we use numerical dominance (Andersen, 1992; Cerdá *et al.*, 1997) to assess the role of dominance hierarchy in the structure of leaf-litter ant assemblages. We chose this method for three

reasons: (1) it is nearly impossible to observe all possible competitive interactions between pairs of ant species in the field, (2) it is an effective method when the objective is to evaluate which ant species are more able to control resources (Andersen, 1992; Parr & Gibb, 2012) and (3) numeric and behavioural dominance are usually correlated (Blüthgen & Fiedler, 2004; Parr & Gibb, 2010).

Each bait station followed the general sampling design, but having a pair of sampling points (baits) at the base of the stemless palm and a pair of baits in the surrounding leaf litter. Therefore, we placed 240 baits at each sampling round. At each baiting station, the first pair of baits (leaf-litter and stemless palm) were collected after 15 min and the second pair after 1 h of exposure on both strata. Baits were composed of 50% sardines in edible oil mixed with 50% cassava flour, arranged in the centre of a 6 × 6 cm square of paper. All ants present on the baits were retrieved and placed in plastic bags for identification and counting.

We attributed dominance values to the most common species that visited the baits offered, using the numerical dominance formula (Santini *et al.*, 2007; Parr & Gibb, 2012):

$$Nd = \left( \frac{D_i}{D_i + S_i} \right)$$

where  $i$  represents each analysed species,  $D_i$  is the number of baits monopolised by species  $i$  and  $S_i$  is the number of baits where species  $i$  was present and subordinate (sharing the bait with other species). Baits were considered monopolised if >20 individuals of the same species were using the bait without another ant species. This index ranges from 0 (fully submissive species) to 1 (fully dominant species). We considered any species with numerical dominance >0.3 to be dominant. The data on the species visiting the baits in the first 15 min included any differences in the capacities to find and monopolize resources. The dominance index was calculated only for species that were collected in at least five baits.

#### Colonization experiment

Five riparian bottomland plots were used as part of the colonization experiment. This experiment also used the paired sampling design of a stemless palm and the open litter at an adjacent area. For each pair, all the vegetation debris at the base of a randomly chosen stemless palm was removed and measured using a graduated bucket. The same volume of litter was then removed from an area adjacent to the palm. The same volume of litter was replaced in the empty spots using previously processed litter. Processed leaf litter was composed of litter collected at other locations (mostly around the Ducke Reserve base), scattered on the sidewalk and exposed to the sun for at least 2 days. Handling the litter and exposure to the sun modifies the microclimate of the leaf litter, forcing potential ant colonies to move. After installation of the experiment, the palm trees and the manipulated areas adjacent to it were marked. In total, 23 pairs were installed, resulting in 46 samples.

Six months after installation 13 pairs were removed; the remaining 10 pairs were removed after 1 year. The first 6 months

encompass only the rainy season (shallow water-table period), and the experimental samples removed after 12 months encompass a full hydrological cycle (i.e. the experiment was removed at the end of the dry season). For both stemless palm trees and adjacent areas, the processed litter was carefully collected and inspected and all ant colonies were collected and counted. Here, we used the presence of reproductive females with brood as an indicator of ant colonies. After the carefully manual search for colonies, all material was processed using Winkler extractors, using the same collection process previously described. Ants can colonize open patches of litter by foundress, by satellite nests of existing colonies or by mature queenright colonies (Kaspari, 1996a). As your sampling does not enable discrimination between colony emigration and colony founding, we used the number of new colonies as a proxy for ant colonization. More than one reproductive female of the same species in the same sample was counted as a single colony.

Each sample was individually labelled and transported to the Zoology Laboratory of the Federal University of Amazonas. In the laboratory, the material was sorted, and ants were separated from other arthropods. Ants were then screened and dry-mounted for identification. Initially, we identified the ants to genus-level using keys available in Baccaro *et al.* (2015). Subsequently, all specimens were identified to species or morphospecies using specialized literature, by comparing with material deposited in the entomological collection of the Instituto Nacional de Pesquisas da Amazônia – INPA and by sending specimens to specialists. The morphospecies were created based on morphological differences of the proximal species. Voucher specimens were deposited in the UFAM Entomological Collection.

#### Data analysis

We investigated different facets of the ant diversity structure in a series of comparisons between the same plots during rainy and dry season (shallow and relatively deep water-table) for each habitat (stemless palm and adjacent leaf-litter). The sample unit was the plot in all analyses. We reduced the dimensionality of our species matrices using a Principal Coordinate Analysis (PCoA) based on Bray–Curtis dissimilarity distance. We were interested in the overall effect of water-table; therefore, we compared the configuration scores (in our case, the plots) of our four ordinations (stemless palm shallow/deep and litter shallow/deep) using Procrustes rotation analysis (Peres-Neto & Jackson, 2001). The Procrustes analysis rotates the ordination matrix scores to maximum similarity with a target matrix by minimizing the sum of squared differences. We then performed a 999-permutation procedure to estimate the significance of the observed correlation in symmetric Procrustes rotation (Oksanen *et al.*, 2019). This analysis shows whether the assemblage composition over the 10 plots presents congruent changes between rainy and dry season in each habitat. We additionally compared the heterogeneity variation of the assemblage composition between the shallow and deep water-table period for each habitat using the analysis of multivariate homogeneity of group dispersions (PERMDISP, Anderson *et al.*, 2006). PERMDISP is

a multivariate analogue of Levene's test for homogeneity of variances. For this, we used the PCoA axis based on Bray-Curtis distance of stemless palm and leaf-litter ant matrixes. In this case, we generated two ordinations, one for the ant species sampled at litter of stemless palms and the other for the ant assemblage samples at the leaf-litter adjacent to the palm. The significance of each test was estimated based on the 999-randomisation procedure.

Ant richness and the occurrence from the Winkler samples of each habitat (litter of stemless palms and leaf-litter) sampled during the rainy season (shallow water-table) and dry season (deep water-table) were compared using paired *t*-tests. We used occurrence as a measure of abundance since it may reflect the number of ant colonies in each plot. Therefore, the abundance of each species varied between 0 and 12 (the same species was collected in all samples of both habitats) per plot.

We also used paired *t*-tests to compare the abundance of the dominant species (estimated by the number of occurrences in each plot) and the total number of monopolized baits at litter of stemless palms sampled in the rainy season and dry season. The same analysis was performed for the leaf-litter adjacent to the palm.

The same analysis structure was used to compare the colonization process. We used paired *t*-tests to compare the number of new colonies, defined by the presence of queens (reproductive individuals) nesting in the litter at the base of stemless palms after six (rainy season only) and 12 months (rainy and dry seasons) from the beginning of the colonization experiment. The same analysis was carried out for the leaf-litter areas adjacent to the palm. The sample unit was the plot in all analyses. All analyses were run in the R environment (R Core Team, 2019).

## Results

A total of 41 907 ants were collected in 766 samples; there were 480 bait samples and 286 samples from litter of stemless palms, leaf litter, and from colonization experiments. In total, 9 subfamilies, 53 genera, and 176 species of ants were identified; among these, 112 species were identified and 64 species were classified as morphotypes. The genera with the highest number of morphotypes were *Pheidole*, *Solenopsis*, *Hypoponera*, and *Strumigenys* (Appendix S2).

### Species composition

The species composition of the assemblages sampled at litter of stemless palms between the two seasons were congruent (Procrustean correlation = 0.76,  $P = 0.003$ , Fig. 2a). Conversely, the species composition of assemblages sampled at leaf-litter during rainy and dry season were much more variable (Procrustean correlation = 0.56,  $P = 0.101$ , Fig. 2b). The assemblage composition heterogeneity followed the same pattern; it was similar at litter of stemless palms (PERMDISP,  $F_{1,18} = 3.364$ ,  $P = 0.083$ , Fig. 2c), compared with leaf-litter (PERMDISP,  $F_{1,18} = 7.069$ ,  $P = 0.015$ , Fig. 2d) during rainy and dry periods.

### Winkler samples

On average, ~10 more ant species were sampled in the leaf litter during dry season (*t*-test,  $t = 2.536$ ,  $P = 0.031$ ; Fig. 3). Conversely, the number of ant species remained fairly similar in the litter of stemless palms (*t*-test,  $t = 1.033$ ,  $P = 0.328$ ; Fig. 3). The ant species occurrence followed the same pattern. The species occurrence in leaf litter during the dry season was approximately 1.5 times higher than the ant species occurrence during rainy season (*t*-test,  $t = 2.633$ ,  $P = 0.027$ ; Fig. 3). In the litter of stemless palms, the occurrence of ants remained similar between the hydrological cycle (*t*-test,  $t = -2.061$ ,  $P = 0.069$ ; Fig. 3).

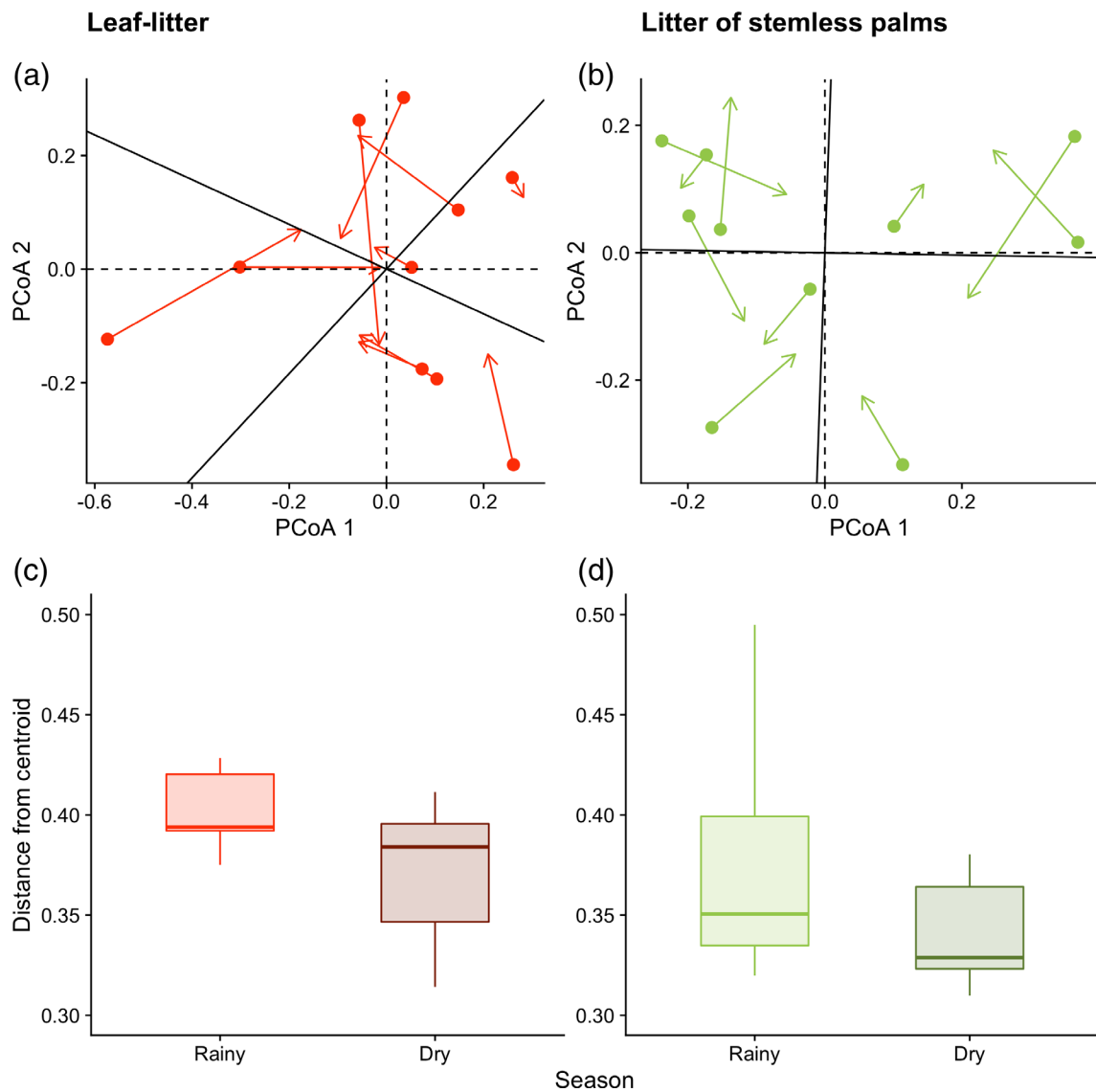
### Dominance

We sampled 52 ant species at baits. The highest number of species collected on the same bait was 5, with an average of 2.8 species per bait. Of the 480 baits offered, 77 were monopolized and 17 were not visited by ants after 1 h of exposure. Only 11 species (*Blepharidatta brasiliensis*, *Crematogaster nigropilosa*, *Gnamptogenys horni*, *Mayaponera constricta*, *Neoponera apicalis*, *N. verenae*, *Nylanderia caeciliae*, and four *Pheidole* morphospecies) were more abundant in the first 15 min of bait exposure. Except by *Nylanderia caeciliae*, these species occurred in less than five baits. Approximately 26% of the species dominated at least one bait, among them, seven species *Crematogaster limata*, *Crematogaster tenuicula*, *Megalomyrmex goeldii*, *Ochetomyrmex semipolitus*, *Pheidole biconstricta*, *Pheidole vorax* and *Pheidole* sp. 8 had a dominance index >0.3 (i.e. monopolized more than 30% of the baits when occurred) and were considered dominant (Table 1).

On average, the number of monopolized baits in leaf litter doubled during rainy compared to dry season (*t*-test,  $t = 3.285$ ,  $P = 0.009$ ; Fig. 4). However, in the litter of stemless palms, the number of monopolized baits remained stable between the periods of the hydrological cycle (*t*-test,  $t = 0.738$ ,  $P = 0.479$ ; Fig. 4). For baits offered on the leaf-litter, the occurrence of the seven dominant species was on average ~2.5 times higher during rainy compared to dry period (*t*-test,  $t = 2.635$ ,  $P = 0.027$ , Fig. 4). By contrast, the occurrence of the seven dominant species remained stable during these periods for communities in litter of stemless palms (*t*-test,  $t = 1.077$ ,  $P = 0.309$ ; Fig. 4).

### Colonization experiment

On average, the number of new colonies was four times higher in the first 6 months (rainy season) in the leaf-litter areas (*t*-test,  $t = -2.131$ ,  $P = 0.05$ , Fig. 5). In one plot, no colony was found in the six experimental leaf-litter patches after 1 year. Meanwhile, the number of new colonies remained constant in the litter of stemless palms between the two periods of the colonization experiment (*t*-test,  $t = -1.359$ ,  $P = 0.245$ , Fig. 5). The ant species that colonized the processed litter are typical of litter samples (Table 2). Among them, only one colony of dominant species (*Pheidole biconstricta*) was found in the leaf-litter habitat.



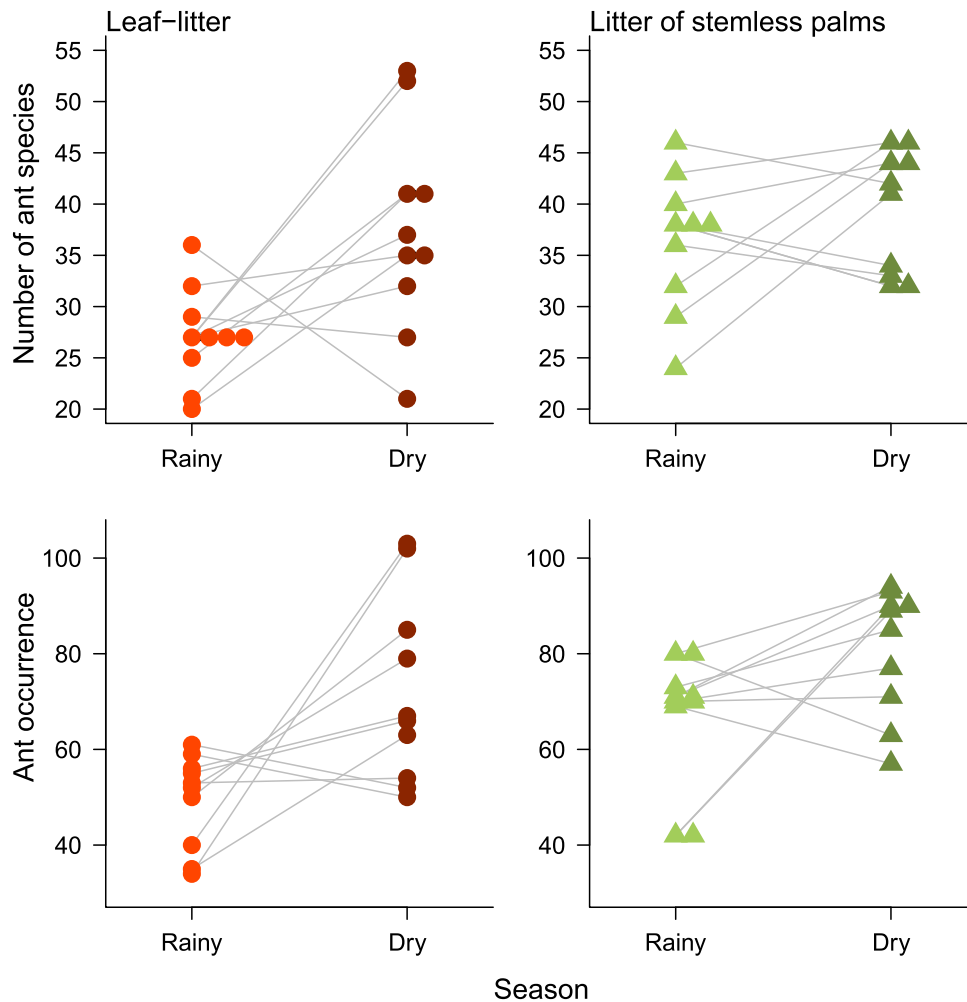
**Fig. 2.** (a,b) Procrustean rotation showing the plots sampled at rainy season (points) superimposed to plots sampled during the dry season (tip of the arrows) for ants sampled at the forest floor and the litter accumulated in the bases of stemless palms. (c,d) Box plot of the distance from the centroid of plots sampled during the rainy season and the dry season for ants sampled at the forest floor and the litter accumulated in the bases of stemless palms at Ducke Reserve, Manaus, Brazil. The lower and upper hinges correspond to the first and third quartiles (the 25th and 75th percentiles) and the bold line represents the median values. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

## Discussion

The water table seems to function as a medium-intensity disturbance for ant assemblages in the valleys of this tropical forest. The leaf litter in plots during rainy (shallow water-table) period harbour less ant richness, lower occurrence, and the assemblage composition was more heterogeneous when compared to the same locations during the dry (deep water-table) season. However, ant activity such as recruitment and investment in resource monopolization seems to follow the moisture availability gradient (Levings, 1983; Dunn *et al.*, 2007), with greater investment in monopolization during the rainy periods when the water table

is shallower and the forest floor in the valleys are soaked. The investments in reproduction follow the same pattern, with more colonies found in the leaf litter during the shallow water table period. All of these changes were strongly decreased or absent for the assemblages sampled in the litter that accumulated at the base of stemless palms. Our results suggest that there will be at least two processes operating. A shallow water table level may act as a disturbance to most ant litter species but may favour ant activity such as resource monopolization and litter colonization.

The effects of water table on occurrence and foraging depends on species characteristics. For example, about 29% of the ant species of Florida coastal plains pine flatwoods are more



**Fig. 3.** Number and occurrence of ant species sampled in leaf litter and at the litter accumulated in the bases of stemless palms during two periods of the hydrological cycle in Ducke Reserve, Manaus, Brazil. Some points were horizontally dodged to improve clarity. The grey lines connect the same plot in the two periods. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

abundant in areas with a shallow water table, up to 37% were more abundant at sites with deeper water-table levels and the remaining 34% of species were not related to water-table level (Tschinkel *et al.*, 2012). This pattern is probably related to adaptations to combat water ingress in their nests or colony movement (Kolay & Annagiri, 2015). Some *Pheidole* and *Solenopsis* species evacuate flooded nests in a rapid and organized manner to minimize the impact of flooding (Morrill, 1974; Wilson, 1986; Longino, 2009; Adams *et al.*, 2011). Therefore, such adaptations may allow species to survive unpredictable floods in places where the water table is more superficial or in periodically flooded areas such as wetlands or riparian zones. While the behavioural responses to nest flooding of *Crematogaster* and *Megalomyrmex* are still unknown, a significant proportion of our dominant species belongs to *Pheidole*; therefore, it is possible that behavioural responses to prevent nest drowning may be operating, favouring the persistence of these species during the shallow water table period. More natural history

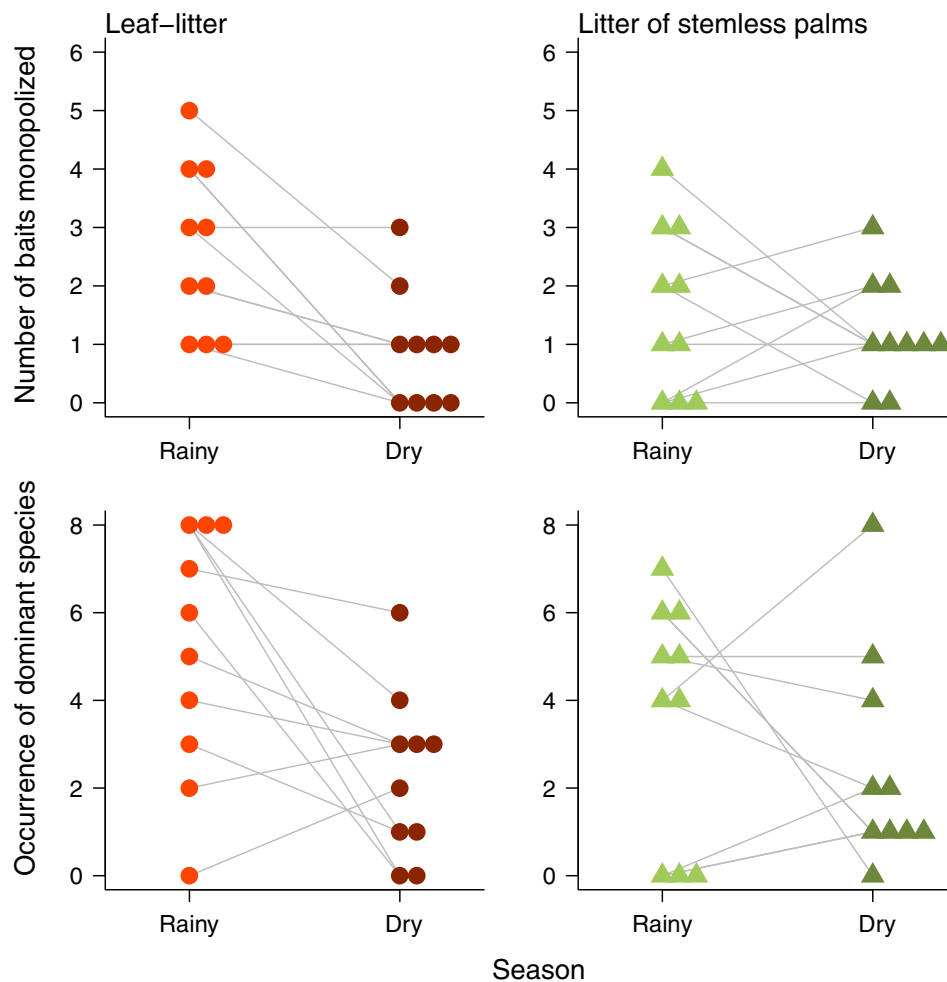
information still needed to unravel the mechanisms that permit some species to cope with frequent flooding of their colonies.

The combination of different adaptations or higher tolerance to flooding is perceptible at the assemblage level. The leaf-litter ant richness and occurrence were higher during the dry season in the leaf litter. Also, this habitat showed a more heterogeneous species composition. At the plot level, the ant species assemblage composition was more unpredictable and more variable along the hydrological cycle compared with the litter of stemless palms. The vertical stratification of litter at the bases of stemless palms makes it less prone to temporal flooding during heavy rains. Our approach of correlative and experimental manipulation reinforces that the groundwater level may be a source of disturbance by favouring unpredictable floods, for the assemblages of ants living in leaf litter.

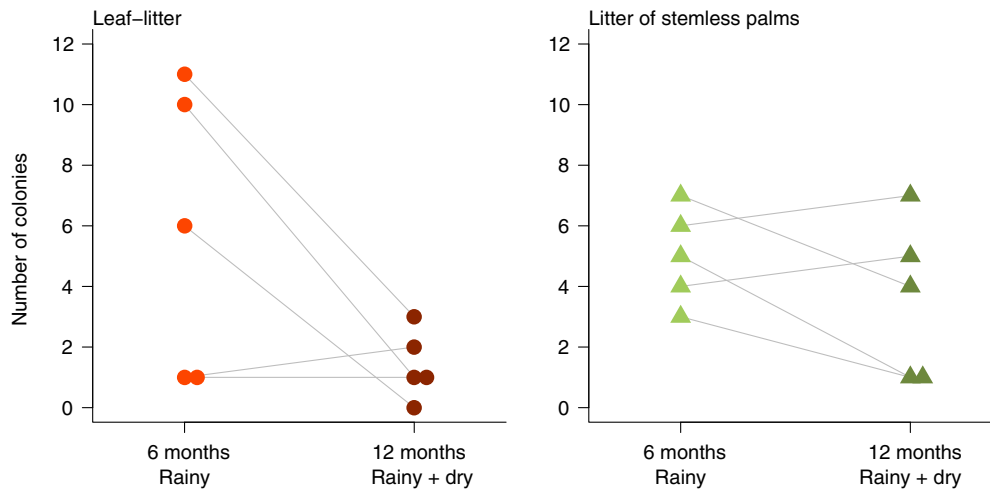
The abundance of dominant species and investment in resource monopolization seems to follow the moisture gradient in the opposite direction of diversity patterns (richness and occurrence). It is tempting to conclude that the lower richness

**Table 1.** Summary of the number of baits on which ant species occurred, the number of monopolised baits after 15 and 60 min of bait exposure for the seven species considered dominant (in bold) and the seven most abundant species that were not considered as dominant.

Species	Number of baits on which the species occurred		Number of monopolised baits		Dominance index
	15 min	60 min	15 min	60 min	
<i>Pheidole biconstricta</i>	7	20	3	14	0.62
<i>Ochetomyrmex semipolitus</i>	1	6	0	4	0.57
<i>Crematogaster tenuicula</i>	19	41	6	23	0.48
<i>Megalomyrmex goeldii</i>	5	11	2	5	0.43
<i>Crematogaster limata</i>	5	13	0	7	0.38
<b><i>Pheidole sp.8</i></b>	2	4	0	2	0.33
<b><i>Pheidole vorax</i></b>	1	5	0	2	0.33
<i>Crematogaster brasiliensis</i>	2	7	0	2	0.22
<i>Nylanderia caeciliae</i>	14	10	1	1	0.08
<i>Pheidole sp.19</i>	2	11	0	1	0.07
<i>Paratrachymyrmex sp.1</i>	6	8	0	0	0
<i>Mayaponera constricta</i>	3	2	0	0	0
<i>Azteca sp.1</i>	2	2	0	0	0
<i>Crematogaster nigropilosa</i>	3	1	0	0	0

**Fig. 4.** Number of monopolised baits and occurrence of dominant species at leaf litter and the litter accumulated in the bases of stemless palms during two periods of the hydrological cycle in Ducke Reserve, Manaus, Brazil. Some points were horizontally dodged to improve clarity. The grey lines connect the same plot in the two periods. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].





**Fig. 5.** Number of ant colonies (i.e. with the presence of queen and workers) after 6 and 12 months of colonization experiments in leaf litter and litter adjoined in the bases of stemless palms in Ducke Reserve, Manaus, Brazil. Some points were horizontally dodged to improve clarity. The grey lines connect the same plot in the two periods. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

and abundance in the leaf litter is the result of higher dominance and higher occurrence of dominant ants; however, we did not find support for this hypothesis (Supplemental material 3). In open savannas, dominance measured with baits scale up to assemblage level (Parr, 2008), but the dominance in tropical forests do not necessarily imply constraints to species richness in leaf litter (Baccaro *et al.*, 2012). Therefore, the dominance reported here may apply to the species sampled with baits only, but it can give some insights about ant activity in general.

Dominant ant species require greater foraging areas to maintain high energy levels. Therefore, a strategy commonly adopted by numerically dominant species is to build polydomous colonies (when a colony inhabits several independent nests). A polydomous colony ensures a larger foraging area (Longino, 2003) and allows a colony to be more competitive in areas with fewer resources (Baccaro *et al.*, 2010). Among the seven species considered dominant in our study, four (*Crematogaster tenuicula*, *Crematogaster limata*, *Pheidole biconstricta*, and *Megalomyrmex goeldii*) have been reported to form polydomous colonies (Longino, 2003; Debout *et al.*, 2007) and a fifth (*Ochetomyrmex semipolitus*) probably also do so (Fernandez, 2003). The proportion of species with polydomous colonies is higher in areas with a shallow water table (Baccaro *et al.*, 2013), suggesting that this behaviour may provide adaptive advantages in an environment that is constantly impacted by water disturbance. Therefore, having the colony divided in small nests scattered over the leaf litter may favour resource location, explaining the higher activity of dominant species and higher resource monopolization.

Another strategy to deal with unpredictable floods is to place the nest in higher spots, such as plants or deadwood. This behaviour seems to be common among the dominant species. Although there are records of *Megalomyrmex goeldii* and *Ochetomyrmex semipolitus* foraging in lower vegetation, the nests of both species were only found in the

litter (Brandão, 2003; Fernandez, 2003). However, the remained four dominant species identified at species level, are known to be able to have arboreal nests. *Crematogaster tenuicula* and *C. limata* are strictly arboreal (Longino, 2003), while *Pheidole biconstricta* and *Ph. vorax* are more generalists nesting in the leaf litter, deadwood and above the ground (Longino, 2009). The arboreal nesting habits or flexibility of nesting strata associated with polydomy may foster important facets of a typical dominant species: have a relative undisturbed nest and larger foraging areas to keep the demands of a larger colony. Would be interesting to know if both facets still present in dominant species in relative drier areas (plateaus) of tropical forests.

We also found a clear signal of the disturbance mediated by the water-table fluctuation in the ant assemblage colonisation dynamics. The number of new colonies was similar at 6 and 12 months in the litter of stemless palms, suggesting that the microhabitats offered was occupied during the first 6 months of the experiment. However, we found a different picture in the leaf-litter patches that are more prone to unpredictable floods. Contrary to our hypothesis, the colonization rates were higher during the rainy season. After a full hydrologic cycle and at the peak of the dry season, fewer colonies were recorded. The roles of competition and predation by dominant species as forces that control colony colonization over time could explain the lower number of colonies after 1 year of the experiment. However, this hypothesis seems less probable because the higher number of new colonies in the leaf-litter during the rainy season match with the higher activity and resource monopolization patterns of dominant species. In addition, we found only one colony from a dominant species (*Pheidole biconstricta*) in the leaf-litter experiment. Therefore, the colonization cycle may be more related to moisture fluctuation, competitive exclusion between non-dominant species, or another biotic factor. In fact, previous work has also found that litter ant colonization is positively related to moisture and negatively related to army ant density

**Table 2.** Ant species and number of new nests (presence of queen with brood) after 6 and 12 months of colonization experiments in leaf litter and litter added in the bases of stemless palms in Ducke Reserve.

Species/morphospecies	Habitat			
	Added litter		Added litter at base of stemless palm	
	6 months	12 months	6 months	12 months
<i>Carebara</i> sp. 1	0	0	0	1
<i>Crematogaster flavosensitiva</i>	1	0	0	0
<i>Cyphomyrmex rimosus</i>	1	0	0	0
<i>Dolichoderus imitator</i>	0	1	0	0
<i>Dolichoderus</i> sp.1	0	0	1	0
<i>Gnamptogenys horni</i>	0	0	1	0
<i>Hypoponera</i> sp. 1	2	0	0	0
<i>Hypoponera</i> sp. 2	3	0	0	0
<i>Hypoponera</i> sp. 5	0	1	1	1
<i>Hypoponera</i> sp. 9	1	0	1	0
<i>Lachnomyrmex</i> sp. 1	0	0	2	0
<i>Mayaponera constricta</i>	0	0	1	0
<i>Nylanderia</i> sp. 5	3	0	0	0
<i>Nylanderia</i> sp. 6	0	0	1	0
<i>Octostruma balzani</i>	0	1	0	1
<i>Pheidole biconstricta</i>	0	1	0	0
<i>Pheidole exigua</i>	2	0	1	0
<i>Pheidole meinerti</i>	0	0	1	0
<i>Pheidole</i> sp. 27	0	0	0	1
<i>Pheidole</i> sp. 4	1	0	0	1
<i>Solenopsis brevicornis</i>	0	0	0	2
<i>Solenopsis castor</i>	0	0	1	0
<i>Solenopsis clytemnestra</i>	0	1	1	1
<i>Strumigenys beebeyi</i>	1	0	0	0
<i>Strumigenys denticulata</i>	11	1	8	6
<i>Strumigenys elongata</i>	0	1	0	2
<i>Strumigenys infidelis</i>	1	0	1	1
<i>Strumigenys</i> sp. 10	0	0	1	0
<i>Strumigenys</i> sp. 4	1	0	2	0
<i>Strumigenys</i> sp. 9	0	0	1	0
<i>Strumigenys trinidadensis</i>	0	0	0	1

(Kaspari, 1996b; Kaspari & O'Donnell, 2003). Our results adds a new facted to this pattern, suggesting that the ant colonization process may be affected by the disturbance caused by water table variation, but might be amplified by army ant raids, which are common in tropical forests (O'Donnell *et al.*, 2007).

Disturbance mediated by the water table appears to decrease species richness and occurrence but increases ant resource monopolization and litter colonization. Taken together, these patterns suggest that ant diversity is related by differential survival along the water table fluctuation. However, these apparently conflicting patterns might be better understood and linked if information about colony size and biomass were included. Given the recurrent disturbance caused by water table variation, it is reasonable to expect that ontogeny of some ant colonies might be synced with water table level fluctuation in these areas. Further studies coupling colony development and disturbance may help sort out the factors regulating litter ant patch dynamics in riparian areas. Understanding the relationship between ant diversity and the local water table is relevant,

as riparian areas are among the most threatened ecosystems in tropical forests (Naiman *et al.*, 2010).

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### Contribution of authors

PMSH and FBB conceived the ideas and methods; PMSH collected the data; PMSH, JLPS and FBB processed biological

material; PMSH led the manuscript writing with contributions from JLPS and FBB.

### Data availability statement

The data that support the findings of this study are openly available in GitHub at [https://github.com/Fabricera/Holanda\\_etal](https://github.com/Fabricera/Holanda_etal).

### Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1:** Graphical representation of paired sampling desing.

**Appendix S2:** List of ant species sampled.

**Appendix S3:** Models statistics for the effects of abundance of dominant species and water table period on the abundance and number of subordinate ant species.

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