ORIGINAL RESEARCH ARTICLE

Patterns of ant activity and nesting ecology depend on flooding intensity in a Neotropical floodplain

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Abstract

Disturbance shapes ecological communities. Frequency, predictability, and intensity characterize disturbances, which select for resistant and/or resilient traits of species. Unpredictable and infrequent disturbance events, especially those with no reliable cues, lack selection strength and have less calculable effects on species assemblages and trait-based species sorting. In a flood plain in Northeast Costa Rica, across sites with varying flood frequency and no reliable cues to signal flooding, we used ants as a focal taxon to assess the impact of disturbance on ant activity and species assemblage. We examined activity patterns such as extent of occupancy of baits and nesting guild (i.e. strata used) that might mediate the effects of stochastic flood events. We hypothesized that the ant community in the most frequently flooded site would be dominated by above-ground nesting ants whose nesting traits make them resilient to inundation. The site with the most frequent flooding had the lowest level of ant presence on baits and differed in species assemblage, as demonstrated by the analysis of similarity, compared with the sites with lower flooding frequency. Neither overall species richness nor richness of species in the above-ground nesting guild differed between sites. However, nesting in trees above flood waters may be beneficial to escape frequent and unreliable flooding of habitats, and, as we hypothesized, there was greater activity of above-ground nesting ants compared with ground nesting ants in the most frequently flooded site. These differences in nesting guilds were diminished in the drier sites.

Keywords Arboreality · Caño Palma · Community ecology · Costa Rica · Flooding · Formicidae

Introduction

Flooding, as an ecological disturbance can be experienced by organisms anywhere along the spectra of predictability and intensity and can shape ecological communities (Pickett & White 1985). How communities respond to disturbances often depends on the timing, duration, extent, and/or disturbance

interval (Poff et al. 1997) – all of which characterize the predictability and intensity of disturbance. Unpredictable floods are capable of extirpating ground-dwelling organisms that cannot escape flood waters (Roeder et al. 2018). Many species occurring in frequently and predictably flooded areas have traits that allow for persistence under flooding (resistance) or quick recolonization post-flooding (resilience). For example, frequent flooding can select for species with flood escaping traits and behaviors such as arboreality (Adis and Junk 2002), moving away from a riverbed (Lytle et al. 2008), and rafting (Adams et al. 2011). The development and utility of these flood resistant behaviors is contingent upon reliable cues signaling disturbance and its intensity, as unreliable cues (e.g. rainfall that does not lead to flooding) lack the consistency to select for such traits (Lytle et al. 2008).

In this study, we examined ant communities across a Neotropical flood plain at three sites that vary in flood frequency and duration. We used ants as a focal taxon because they have a variety of traits associated with resilience and resistance to disturbance including vertical stratification of nesting sites (i.e. nesting locations can span below to above

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ground, Hölldobler and Wilson 1990), dispersal ability, and colony founding strategies (Keller 1991; Hamidi et al. 2017). Nesting behaviors, symbioses, and feeding ecology have been described for many Neotropical ants, including nesting behaviors in riverbanks and a diversity of other habitats (Weber 1947). Certain ant species exhibit specialized behaviors promoting persistence flooded areas. For example, some species build levees to make colonies resistant to weak floods (LeBrun et al. 2011), others decrease respiration rate inside the nest (Nielsen et al. 2006), some species secrete water from the nest after floods (Maschwitz & Moog 2000), and others nest in river banks (Ramón et al. 2013). Many ants can survive strong floods by escaping to the canopy or, in case of fire ants, use rafting behaviors (LeBrun et al. 2007). This suggests that the species assemblage in flooded areas reflect selection pressures for species with such adaptations.

The area of study, located in Northeast Costa Rica, floods multiple times each year as a result of rains falling inland which then flow downstream, toward the coast, flooding the North-easternmost coast of the country. Because of the vast area draining slowly to this region, rainfall at the site is not a reliable cue to forewarn flooding events. We sampled ants across sites with different flooding regimes due to small-scale topographical variation (see methods, Lewis et al. 2010) to test the effects that flooding frequency and duration have on ant activity and species assemblage with respect to diversity, richness, species composition, and nesting preferences. We predicted that the most frequently flooded site would be the least species rich and harbor more above-ground nesting species. Previous research demonstrated decreases in abundance of ground nesting ants in frequently flooded areas (Mertl et al. 2009), and lower species richness (Vasconcelos et al. 2010), but an increase of arboreal nesting ants in a flooded Amazon forest (Majer and Delabie 1994). This study explores ant activity and species composition of a seldom studied region of Costa Rica with respect to the unique flooding regime of the area and nesting ecology of ants. The uniqueness of this region, its extreme variability of flooding at a fine spatial scale and lack of reliable environmental cues to signal flooding disturbance permits the contrast of plausible mechanisms that explain how flood disturbance affects ant activity and diversity.

Methods

Study site

We conducted this study in the Barra Del Colorado Wildlife Refuge in Northeast Costa Rica (10°46'N & 38°35'W). The study site is situated in the southernmost region of the refuge, on the property of Caño Palma Biological Station (CBPS) and around the base of a hill (Cerro Tortuguero, hereafter referred

to as Cerro) on the opposite side of the canal bordering the station. The entire region is classified as tropical wet rainforest (Holdridge 1967) and is dominated by flood-resistant palms (further site details in Lewis et al. 2010 and Khazan et al. 2016). At a local scale, there is variation in flooding intensity and frequency consistent with a change in dominance of palm species (Lewis et al. 2010) due to extremely small topographical variation. Rainfall in the region, both at the station and inland, peaks in December and July (CPBS unpublished data) which corresponds with an increase in flood likelihood (Myers 1981), though local rainfall is often decoupled from flood events.

We established transects in areas with frequent, moderate, and minimal flooding regimes (Table 1). We visited all sampling sites regularly (12 months per year, 3–4 days per week during regularly scheduled surveys performed by CPBS researchers) and documented presence and absence of flood waters. These sites in order from most to least frequently flooded are henceforth noted as CP Wet (Caño Palma Wet), CP Dry (Caño Palma Dry), and Cerro. The depth the of Caño Palma canal can be used as a proxy for flooding of the different sites. The CP Wet site is always at least moderately flooded when the canal reaches 1.8 m and the CP Dry site is flooded when the canal reaches 2.0 m in depth. The Cerro floods extremely infrequently, and those flooding events are also monitored thanks to regularly scheduled surveys associated with additional CPBS research programs (described above). The biological station collects data on canal depth twice daily. Using canal depth as a conservative metric, we calculated the number of days flooded in each area in 2014 and 2015 (Table 1).

Ant sampling

We sampled ants in October 2015, two months after the most recent flood which affected both sites on CBPS property, under non-rainy, non-flooded conditions. In each site (frequent, seldom, and extremely rare flooding), we set up three plots each containing a pair of 30 m long and 1.6 m wide linear transects that cross each other, forming a '+', with the centroid of each plot in each site separated by at least 200 m. Each plot was sampled once, so each site was sampled on three different days. Based on the size, design, and placement of transects, each site's sampling area (i.e. area sampled within each of the three sites) was approximately 1800 m^2 (3 transect line pairs covering ~600 m^2 each). Along each transect, we baited all woody vegetation at breast height, the intersection of ground and arboreal communities, to attract both above-ground and ground nesting ants (Yanoviak and Kaspari 2000). While we baited all available vegetation, because of differences in density of woody plants between sites, numbers of baits differed across sites. This was accounted for in analyses (see Statistical Analyses). After one hour we counted the number of workers

Table 1 Frequency and duration of flooding events across the three sites

Site	Days Flooded		# Flood Events		Avg. flood duration (days) ± SD	
	2014	2015	2014	2015	2014	2015
Cerro	0	2	0	1	0	0.01 ± 0.10
CP Dry	43	27	7	10	5.62 ± 5.71	4.14 ± 1.77
CP Wet	71	52	12	10	10.14 ± 8.45	5.40 ± 5.23

for each species present on each bait and hand collected at least one individual of each species to preserve in ethanol. We used baits to measure ant diversity and activity (Bestelmeyer et al. 2000) consisting of a 1 tsp. mix of two common baits, tuna and honey. This bait type offers protein, lipids, carbohydrates, and salt, it is easily smeared on surfaces, and it can be made with consistent composition.

Ants were grouped based on their nesting location (vertical stratum) using available records (http://ants.biology.utah.edu/AntsofCostaRica.html and personal observations. At present, this is the only and most comprehensive resource available on Neotropical ant nesting habits. We categorized ants according to the following categories: ground nesting (including soil and litter nesting species), above-ground nesting (including understory vegetation and canopy nesting species), generalist nesting, and unknown nesting for some taxa which we could not identify to the species level (e.g. *Solenopsis*, *Pheidole*) or whose nesting ecology is not well documented. In this classification we focused on the nest site location, as nests can be destroyed by floods. Foraging is not limited with the nesting stratum as ground nesting ants can forage in the canopy and vice-versa.

Our baiting method effectively attracted ants that nest in various forest strata (Bujan et al. 2016). For example, ants nesting at the base of a tree are able to climb the relatively short distance up a tree when attracted to a food source (e.g. bait). Baiting is efficient and easily repeatable, however some ants (e.g. fungus growers, specialist predators, and subdominant ants) are rarely attracted by baits (Bestelmeyer et al. 2000). Because ants are sensitive to temperature (Porter and Tschinkel 1987; Cerda et al. 1997; Bestelmeyer 2000) we took measurements of ambient temperature (Kestrel 3000) at the start and end of bait placement and ant collection. Temperature did not differ among the three sites ($F = 0.30$; $p = 0.74$).

Statistical analysis

All analyses were performed using R version 3.3.3 unless otherwise stated. We tested for differences in composition of species assemblages (identity of species in assemblages across sites) and ant activity across sites. We calculated Chao 2 estimates (Chao 1984), using presence/absence data of ants on baits because ant abundance can depend on the vicinity of the colony, and can thus bias analyses (Longino et al. 2002). We generated rarefaction curves using baits as the unit of measure in each site to further examine saturation of the community of ants.

Using presence/absence data, we performed a generalized linear model (GLM) with a binomial distribution to test for differences in occurrence across sites. The overall significant GLM was followed by pairwise comparisons using generalized linear hypothesis tests (i.e. post-hoc pairwise comparisons using Tukey contrasts). A GLM was employed as opposed to an ANOVA because the response variable (ant presence/absence) was binomial in nature. We performed chi-square tests to determine if there were differences between sites with respect to nesting guild. For these analyses we used the proportion of baits occupied by each of the nesting guilds in each habitat type (Fig. 2).

We used presence/absence data of ants on baits to test for differences in ant species assemblage across sites by performing an analysis of similarity (ANOSIM) (Olsgard et al. 1997; Rees et al. 2004). This is a non-parametric test for analyzing multivariate (community) differences between groups using the Raup-Crick dissimilarity, a distance metric specific to binomial presence/absence data (Raup and Crick 1979). As our bait sample sizes were uneven across sites (see above, 112 in CP Wet, 194 in CP Dry, 185 in Cerro), we randomly sampled 100 baits (with replacement) from each site to perform the ANOSIM (an analysis with 1000 permutations) and repeated this process 500 times. We performed pairwise ANOSIM using the statistical software PAST v3.21 (Hamer et al. 2001) and report the test statistic ± SD for ten repeated tests which each used 100 randomly selected baits from each site, as described above. Many fewer bootstraps were performed for pairwise ANOSIM because of software limitations and the lack of differences in test statistics and p values across runs.

To follow up the ANOSIM and examine which species drove the differences in species composition among sites, we performed a SIMPER (similarity percentage) analysis. SIMPER uses Bray-Curtis distances to calculate the average dissimilarity among pairs of sites and the contribution to the dissimilarity by each species. Because of the sensitivity of SIMPER analyses to pseudoreplication, and because the analysis employs Bray-Curtis distance matrices, we used transect (~600 m²) as our unit of replication as opposed to baits. As

Table 2 Ecological diversity indices calculated using species presence/absence data at each bait. Nesting strata color scheme as defined in figs. 2,3

Site	Evenness	Observed Species Richness	Richness by Nest Strata Above-ground Generalist Ground Unknown	Chao 2 estimate
Cerro	0.571	23	6 11 3 3	23.81 ± 3.62
CP Dry	0.523	22	7 12 2 1	24.67 ± 6.32
CP Wet	0.552	22	5 8 5 4	30.42 ± 8.99

such, we derived an index of the spatial coverage of each species (hereafter 'occupancy') defined as the number of baits per transect line at which ants of a given species were present (i.e. summation of presence/absence of each species across all baits in each transect). Finally, to test our prediction that the ant assemblage of the CP Wet site would be dominated by above-ground nesting ants, and to test for differences in nesting strata within sites, we performed chi-square tests across sites and within sites. Here we used occupancy data for each site for each chi-square test to test the evenness of the communities with respect to nesting strata.

Results

In total, we sampled 591 baits (breakdown across sites stated above) and found that ecological diversity metrics such as richness and evenness were comparable across all sites (Table 2). Based on the rarefaction curves (Fig. 1) and the similarity of observed richness and Chao 2 estimates, we have good evidence that we sampled the whole ant community in each of our sites. However, since this study intersects geography with phylogeny (Fauth et al. 1996) and because our sampling protocol limits our ability to speak to species interactions, we use species assemblage, as opposed to community throughout. Ant activity as determined by presence of ants on baits differed significantly between sites (GLM: $z = 4.945$, $p < 0.001$), with the wettest site (CP Wet) containing the lowest ant activity compared to the other sites (Table 3, $z = -2.298$, $p = 0.022$). Nesting guild occurrence on baits differed across sites ($\chi^2_{(df=6)} = 58.381$, $p < 0.001$; Fig. 2). The occupancy of nesting guilds differed between CP Wet and Cerro ($\chi^2_{(df=3)} = 38.268$, $p < 0.001$) and CP Dry and Cerro ($\chi^2_{(df=6)} = 40.357$, $p < 0.001$), and less drastically between CP Wet

and CP Dry ($\chi^2_{(df=6)} = 7.593$, $p = 0.055$). Contrary to our expectations, we found the same number of ground and above-ground nesting species (5 species of each category) at our wettest site.

In terms of ant activity by nesting guild, our wettest site, CP Wet, was comprised of 37.3% above-ground nesting ants compared to 14.9% ground nesting ants. Despite the fact that two guilds were equally speciose in this site, above-ground nesting ants were more widespread across baits than ground nesting ants (Fig. 2). Above-ground nesters occurred on more baits than ground nesting ants at our drier sites as well (Fig. 2; CP Dry: 29.4% and 3.1% respectively, Cerro: 8.1% and 3.2% respectively), implying overall greater occupancy and activity
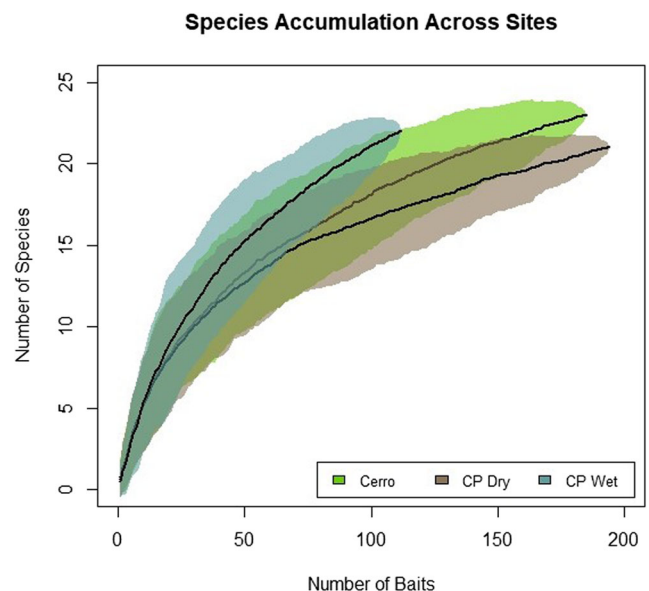

Fig. 1 Species accumulation curves for each site using bait as the sampling unit

Table 3 Ant activity at each site as determined by ant presence on baits. Post-hoc pair-wise comparisons (generalized linear hypothesis test) of presence/absence data compare activity between sites

Habitat	% Baits with ants present	Comparison	p value (post-hoc test)
Cerro	68.6%	CP Dry < Cerro	0.998
CP Dry	68.6%	**CP Wet < CP Dry**	**0.047**
CP Wet	55.3%	**CP Wet < Cerro**	**0.056**

by above-ground nesting ants compared to ground nesters. At Cerro, our driest site, generalist ants were most active and had the widest spatial coverage across baits, as they were present on 64.3% of baits at that site.

Our multivariate community analyses indicated that different species assemblages exist among sites with different flood regimes (ANOSIM global R; mean of 500 permutations ± SD: 0.028 ± 0.006; $p < 0.001$). Pairwise ANOSIMs demonstrate significant differences in the ant assemblage across all three sites (Table 4). Our SIMPER analysis, which attributes species-specific contributions to dissimilarity between sites, shows pairwise differenecs at the species level between sites (Table 4). Species that influenced the community dissimilarity include *Solenopsis* JTL 007, a nesting generalist, in CP Dry

and Cerro, whereas *Crematogaster longispina*, an above-ground nester, was encountered more in CP Wet.

Discussion

We hypothesized that because of the frequent yet unpredictable flooding encountered in CP Wet, and at times in CP Dry, the ant communities would be predominantly composed of above-ground nesting ants since their nesting strategy is resistant to flooding events. Our study suggests increases in proportional activity of above-ground nesters from dry to wet sites (Fig. 2). Generalist nesting species contributed most to the dissimilarities in species assemblage observed between CP

Fig. 2 Proportion of baits occupied by each nesting strata guild at each site (ordered from driest to wettest).
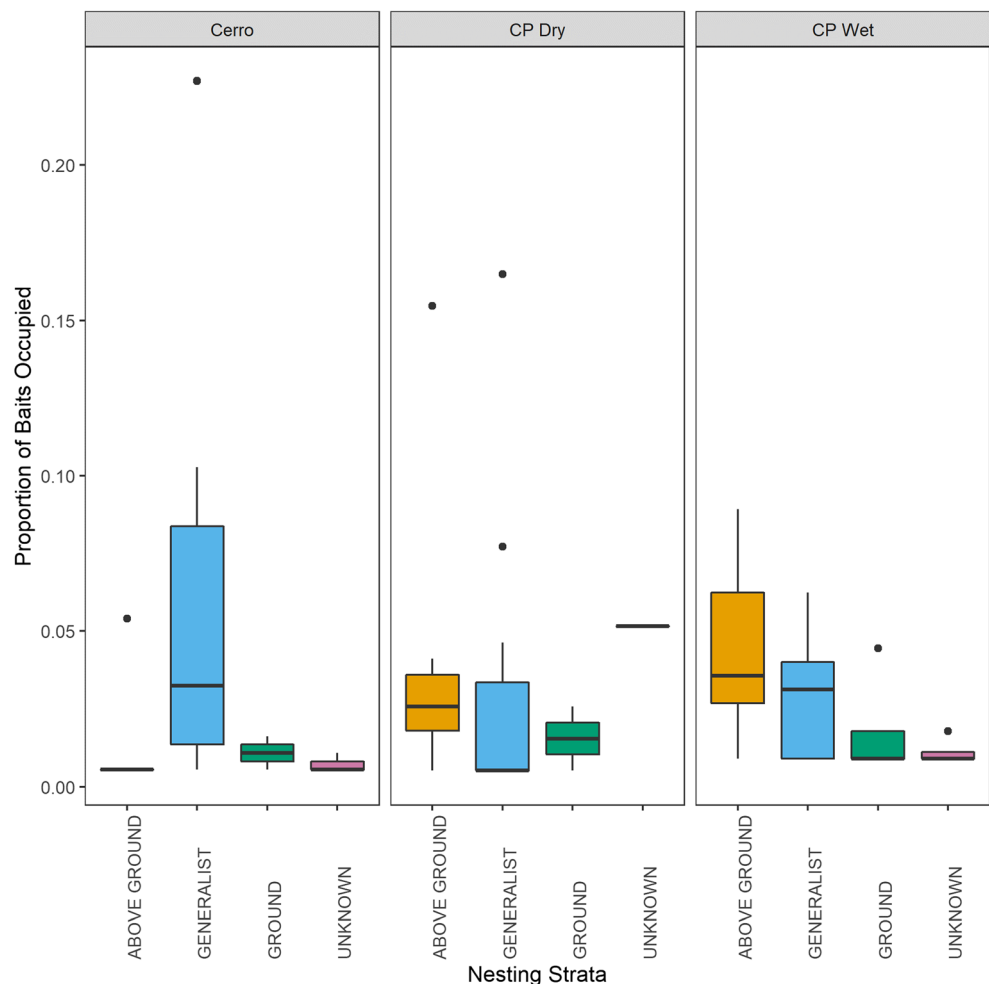
Table 4 Results of the similarity percentage (SIMPER) analysis limited to the top six species driving dissimilarity between sites (and contributing at least 5% to the dissimilarity). Pair-wise analysis of variance (ANOSIM) results between sites with ANOSIM Global R and Bonferroni adjusted p value based on 10 random samples of 100 baits in each site. Nesting strata color scheme as defined in figs. 2,3

| CP Wet vs. CP Dry (Global test, R = 0.034, p = 0.0006) Average dissimilarity = 85.24%				
Species	Average occupancy CP Wet	CP Dry	Contribution to dissimilarity %	Nesting ecology
Azteca nigra	1.16	5.00	17.10	Above ground
Solenopsis JTL007	0.50	5.33	16.40	Generalist
Tapinoma melanocephalum	0.17	2.50	8.35	Generalist
Crematogaster longispina	1.66	1.00	6.34	Above ground
Unknown	0.17	1.00	5.64	Unknown
Azteca instabilis	0.67	1.33	5.39	Above ground
CP Wet vs. Cerro (Global test, R = 0.046, p = 0.0005) Average dissimilarity = 85.54%				
Species	**Average occupancy CP Wet**	**Cerro**	**Contribution to dissimilarity %**	**Nesting ecology**
Solenopsis JTL007	0.50	7.00	21.20	Generalist
Pheidole anastasii	1.16	3.16	9.24	Generalist
Nylanderia JTL006	0.67	3.00	9.09	Generalist
Crematogaster carinata	0.00	2.16	7.19	Generalist
Azteca instabilis	0.67	1.16	6.29	Above ground
Crematogaster longispina	1.16	0.00	6.05	Generalist
CP Dry vs. Cerro (Global test, R = 0.045 ± 0.009, p = 0.0005) Average dissimilarity = 73.17%				
Species	**Average occupancy CP Dry**	**Cerro**	**Contribution to dissimilarity %**	**Nesting ecology**
Solenopsis JTL007	5.33	7.00	15.3	Generalist
Azteca nigra	5.00	0.166	14.00	Above ground
Pheidole anastasii	0.00	3.16	8.97	Generalist
Nylanderia JTL006	1.50	3.00	6.80	Generalist
Tapinoma melanocephalum	2.50	1.00	6.61	Generalist
Azteca instabilis	1.33	1.66	6.35	Above ground

Wet and Cerro whereas the dissimilarity in species assemblage between CP Wet and CP Dry was explained by both above-ground and generalist species. That assemblage dissimilarity between the wet and two dry habitats is derived from two nesting guilds (above-ground and generalist) both of which have above-ground nesting capabilities, lends further support of the important role of arboreality in nesting in dealing with flood disturbance. This trend, however, was tempered by the fact that we observed more species, albeit with limited occupancy, of ground nesting ants in the wettest site compared to the drier sites (Table 2). Arboreality can increase species resilience to environmental disturbance (Scheffers et al. 2017), and our study corroborates this finding in that species that use above-ground nesting or other more generalist nesting behaviors (i.e. generalists), successfully persist in frequently flooded areas. Another study to test effects of flooding on ant communities with respect to flooding frequency also found differences in species assemblage and abundance across habitats with different flood regimes, but those authors examined only ground nesting species (Mertl et al. 2009).

In our drier sites, generalist nesters were the dominant, most active guild whereas in more flooded habitats, the above-ground nesting guild outnumbered generalist ants (Fig. 3). Above-ground nesting ants only became dominant when generalist ants, some of which can also climb, were reduced in numbers as denoted by the activity, or extent of occupancy of ants on baits. These differences could also be perpetuated by traits of resilience including differential dispersal and colony establishment abilities of ants of different nesting strata; something that should be explored at the species-level scale. Baiting might overlook species which are good at bait discovery and get displaced by dominant ants after an hour (Davidson 1998). However, baits are frequently used for assessing community level responses in ants (Bujan et al. 2016; Fowler et al. 2014; Peters et al. 2014; Kaspari et al. 2008), and we are confident that we sampled majority of the species in our community (Fig. 1)."

Drier sites had higher occurrence of *Tapinoma melanocephalum*, a tramp species often recorded around human structures and disturbed habitats, but commonly found in pristine habitats of the New World tropics (Wetter 2009). Our sampling was done about 1 km away from the field station, but in general the study area is not densely populated or urbanized, so we are confident that these ants were coming from established forest populations. Although this species often inhabits disturbed habitats, flooding disturbance seems to be unfavorable as *T. melanocephalum* occurrence was lower in the frequently flooded forest (Table 4). This suggests that

Fig. 3 Proportion of baits occupied by each species at each site arranged by nesting strata
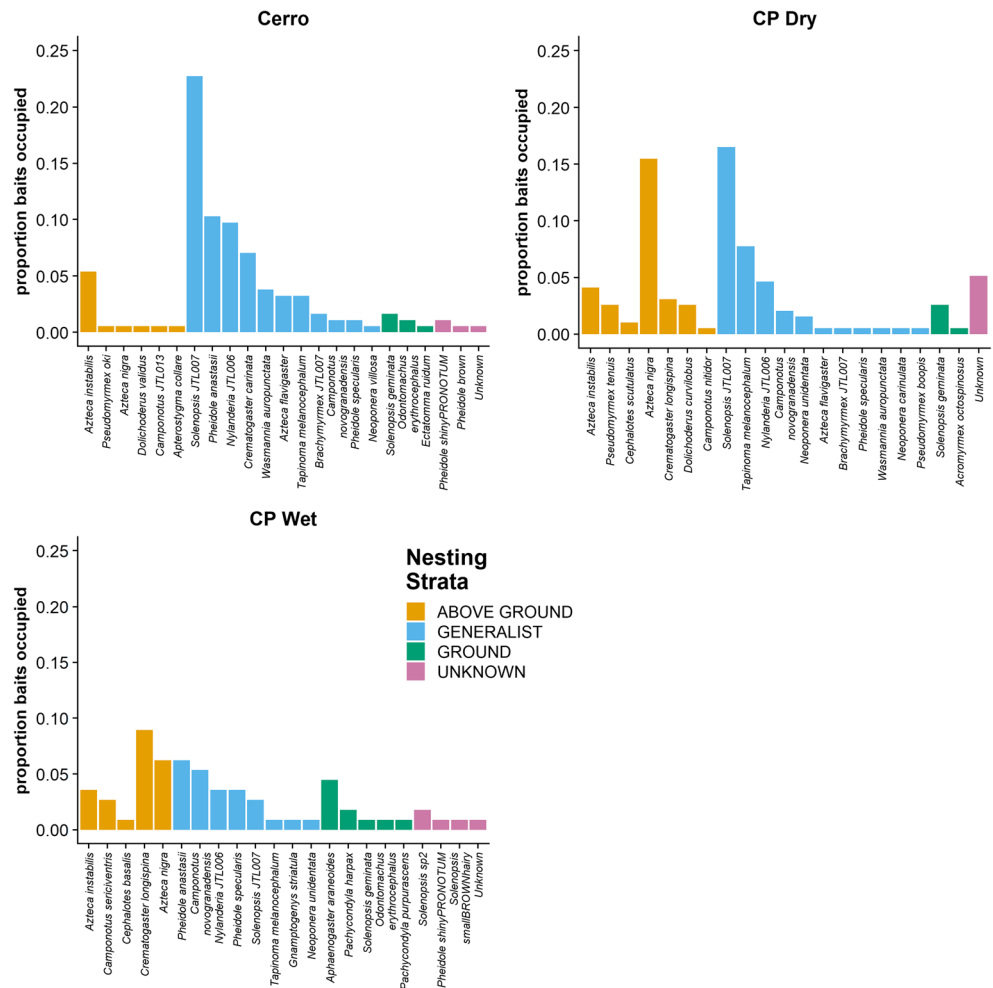
native ants at the flooded site are less likely to compete for resources with the invasive *T. melanocephalum*.

While, as seen in Fig. 2, our data demonstrate a trend toward more above-ground nesters in the wettest habitat compared to drier habitats, and most generalist ants in the driest habitat, these trends were obscured by the number of species present from each guild (discussed above). This unexpectedly high number of litter-nesting ants in the wettest habitat can be explained in two ways: 1) since sampling occurred two months after the last flood, these species had enough time to re-establish themselves, and/or 2) the ground nesting species we encountered are able to respond to disturbance with some unaccounted flood resistant behaviors such as moving the nest vertically or rafting. These explanations could be explicitly tested using time-series data and studying the behaviors of each species.

First, the spatial coverage and activity of ground nesting ants was suppressed at wet sites (i.e. ants were present on fewer baits in the wet compared with drier habitats). Thus, although ground nesting ants recolonized after, or persisted through floods, they may have not had sufficient time to reach high abundances. In the case that two months of no floods

allowed ants to re-colonize previously flooded habitats, we would also expect some community convergence between sites, especially considering that our sites were relatively close with few barriers to disrupt the probability of occurrence (colonization). Yet, we found strong assemblage dissimilarity across sites indicating that communities have not converged. Additional sampling methods, such as paired canopy and ground pitfall traps, would increase the number of recorded species, but each additional method has downsides (Gotelli et al. 2011), which is why we opted for a single standardized method capable of capturing representative species from all designated nesting guilds. Second, two of the most active ground nesting species in the CP Wet habitat, are known to exhibit flood resistant traits. For example, nests of *Pachycondyla harpax*, which builds subterranean nests, also builds nests in extremely wet areas such as lake shores and the bottom of riverbeds (Mitchell and Pierce 1912). Their ability to nest in flood prone areas, corroborated by our study, indicates that these ants have some behavioral and/or physiological adaptation that permits their survival in dynamic environments. Similarly, *Aphaenogaster araneoides*, the most common ground-nester in the flooded habitat, absent from the

drier sites, has demonstrated adaptations to survive frequent flooding. This ant is known to frequently relocate nests as a result of environmental conditions and resource availability (McGlynn et al. 2004). Perhaps this species reacts similarly to cues of flooding (i.e. water at the nest entrance) and can flee vertically to escape the flood.

Understanding the immediate effects of floods and reestablishment of species assemblages would require time-series sampling. Time-series data would provide invaluable information on community succession and should be coupled with species-specific studies focusing on the natural history and ecology of these little studied ant species. More fine-scaled natural history information on species' behaviors including nesting location, foraging method, colony size, etc. will be further explain the spatial patterns of ant colonies, and the ability of species to colonize and thrive in variable environments like floodplains.

In summary, the species assemblages and activity of ants differ across habitats which are spatially close and differ primarily in flood frequency and intensity. Our findings of differences in nesting ecology across a differentially flooded region demonstrates the robust nature of ants and their diverse abilities to survive and thrive in frequently disturbed environments, a phenomenon that will benefit from more trait-based research.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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