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Induced drought in an Amazonian forest affects diversity but not foraging distance of generalist ants

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Abstract

1. Ongoing environmental change is forecast to lead to lower precipitation and concomitant species losses in tropical regions. These losses may affect generalist species that provide essential ecosystem services, such as controlling the rate at which nutrients become available for uptake by other organisms in tropical forests.
2. Here, we use a long-term (16 years) rainwater exclusion experiment in a primary Amazonian tropical rainforest (Caxiaunã National Forest, Northern Brazil) to test whether induced water stress ("drought") affects the species richness of generalist ants, their abundance (i.e., nest density), and the distance at which they detect food resources (i.e., baits).
3. The number of generalist ant species and colonies was reduced by 50% in the drought-induced plot, and ant species composition differed between the control (typical moist forest) and drought-induced plots. Although ants that nested in both control and drought plots had shorter estimated foraging distances than habitat specialists, the distance at which these colonies detected baits was not affected by drought.
4. We conclude that the extremely high diversity of tropical forest ants may be able to buffer the detrimental effects of drought on the resource detection rates of generalist ants. Different generalist ant species were also functionally similar to wet-forest species that cannot forage under drier conditions.

KEYWORDS
climate change, distance to nest, environmental context, ESECAFLOR, Formicidae, resource removal

INTRODUCTION

In many regions, reduction in water availability because of climate change is associated with loss of biodiversity and negative impacts on ecosystem functions (e.g., Phillips et al., 2009; Davidson et al., 2012; IPCC, 2013). For example, increasing drought in tropical forests can lead to hydraulic imbalances that kill larger trees (da Costa et al., 2017; Meir et al., 2015; Meir et al., 2018; Olson et al., 2018), reduce litter inputs, and alter microclimatic conditions of different forest layers where insects currently thrive. Projections forecast a long-term reduction in rainfall in tropical forests, including large portions of the Amazon forest (Flores et al., 2024), but comparatively little is known about the effects of this increasing drought on invertebrate diversity and distribution, and subsequent effects on ecosystem services they provide directly or mediate (e.g., Almeida, Silva, et al., 2023; Baccaro et al., 2013; Costa et al., 2018; Diamond et al., 2012; Sánchez-Bayo & Wyckhuys, 2019). For example, the absence of termites in areas that undergo extended periods of drought can

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reduce litter decomposition and soil moisture retention (Ashton et al., 2019).

In tropical moist forests, ants represent up to 25% of animal biomass in the soil (Hölldobler & Wilson, 1990; Schultheiss et al., 2022), and litter-dwelling ants are particularly affected by drier conditions (Almeida, Silva, et al., 2023; Hood & Tschinkel, 1990). Ants also increase their activity in wetter habitats (Kaspari & Weiser, 2000; Lasmar et al., 2021). Although it is unclear what determines this increase in activity, recent evidence suggests a positive relationship between ant species richness and foraging activity (Lasmar et al., 2021). Thus, understanding the relationship between ant species richness and their foraging activity will be essential for clarifying the role of species loss on the ecosystem services they provide. Indeed, ants perform numerous ecological functions (Del Toro et al., 2012; Silva & Brandão, 2014), including cycling of nutrients and incorporating organic matter into soils (Elizalde et al., 2020).

Ants are also considered the most important removers of resources that reach the litter of tropical forests (Griffiths et al., 2018), where "resource removal" is defined as the displacement of any material used as food (and includes seed dispersal; Anjos et al., 2019; Oliveira et al., 2019), redistribution of nutrients, decomposition, and soil modification. In the absence of ants, no other organism (including small mammals or other insects) can completely compensate for these ecosystem processes (Fernandes et al., 2024). Among ants, resource removal is performed predominantly by a species-rich group of omnivores (Griffiths et al., 2018). However, these diet-generalists can be affected by water availability and they are less abundant in the drier areas of moist tropical forests (Almeida, Silva, et al., 2023; Baccaro et al., 2013).

Importantly, prolonged drought may act as an environmental filter, reducing richness, increasing species replacement (turnover), and selecting for ant species with greater drought tolerance (Almeida, Silva, et al., 2023; Parr & Bishop, 2022; Ribeiro-Neto et al., 2023). For example, species with smaller bodies have smaller foraging ranges (Byrne, 1994) and tend to be less affected by increased temperatures (Gibb et al., 2018). Furthermore, the same ant species may have different niche breadths in different environments, which can alter their behaviour, temporal activity, and realised food niche (Del Toro et al., 2015; Houadria & Menzel, 2020; Krapf et al., 2023). In general, the foraging distance of ants from their nests to any given resource rarely exceeds two meters (Baccaro & Ferraz, 2013; Byrne, 1994) and, therefore, nest density, together with their spatial arrangement, may be a major determinant of the efficiency of ants in using and removing resources at the soil surface. Although changes in the frequency of generalist ants are well-documented to be determined by decreased soil moisture and increased temperature (Bujan et al., 2022; Diamond et al., 2016), we would also expect changes in foraging activity and distances to accompany drought (Lasmar et al., 2021; Oliveira et al., 2019).

Here, we assessed whether a guild of generalist ants that removes resources on the soil surface is altered by experimentally induced drought in an area of primary forest in the eastern Amazon, a region expected to face extreme droughts in the near future (Fisher et al., 2007; Meir et al., 2018). Since the availability of water in tropical forests changes the habitat structure (Almeida, Silva, et al., 2023) and soil microclimate (Baccaro et al., 2013), modifying resource availability and quality for ants (Kaspari & Weiser, 2000; Tsang et al., 2020), we hypothesised that (i) drought modifies the assembly of foraging generalist ants by reducing species richness and the number of colonies, and modifying species composition; and (ii) drought reduces the distance of resource detection by generalist ants. This second hypothesis is based on the understanding that environmental stress caused by drought can negatively affect ant activity because of physiological constraints (Costa et al., 2018; Kaspari & Weiser, 2000; Parr & Bishop, 2022).

METHODS

Study area

The study area is the ESECAFLOR (long-term "Effects of forest drought" experiment; Meir et al., 2018), located at the Estação Científica Ferreira Pena (ECFPn) within the Floresta Nacional (FLONA) de Caxiuanã, Pará, Brazil (Figure 1a; 01° 43′ 05″ S, 51° 27′ 36″ W). Average air temperature at ECFPn is ≈26°C, and the daily variation in temperature is <4°C. The *terra firme* forest on yellow oxisol soils in FLONA is 10–15 m above river level. Average annual precipitation is 2000–2500 mm, but <100 mm/month falls during the dry season (June to November) (de Ruivo & Cunha, 2003).

ESECAFLOR includes a pair of 1-ha (100 × 100-m) plots (Figure 1b). In January 2002, plastic panels were installed 2 m above the soil in the experimental plot to exclude ≈50% of precipitable water (Figure 1d). This reduction has simulated the long-term forecast for the region under the current climate-change trajectory (Flores et al., 2024). Panels are maintained regularly; accumulated plant litter is removed and spread evenly on the ground below each panel. Fifty meters away from the experimental plot, an equivalent 1-ha control plot, whose topography, soil type, and vegetation structure were like that of the experimental plot, was demarcated (Fisher et al., 2007; Meir et al., 2018).

The ESECAFLOR is an ambitious and costly project in terms of setup and maintenance, located in a remote area of primary rainforest in the Amazon Basin. As is often the case with large-scale manipulative studies, the ESECAFLOR has some limitations. Most notable is that it is the only large experiment at the site, and the 1-ha experimental treatment and 1-ha control plot are not replicated. Despite the sampling design, there was no overlapping of the transects (i.e., recording the same ant colony), given the relatively short foraging distance of most ant species in the region (Baccaro & Ferraz, 2013).

Ant sampling

Ants were sampled in two campaigns (September 2017 and February 2018; dry and wet seasons, respectively), always between 09–11 and

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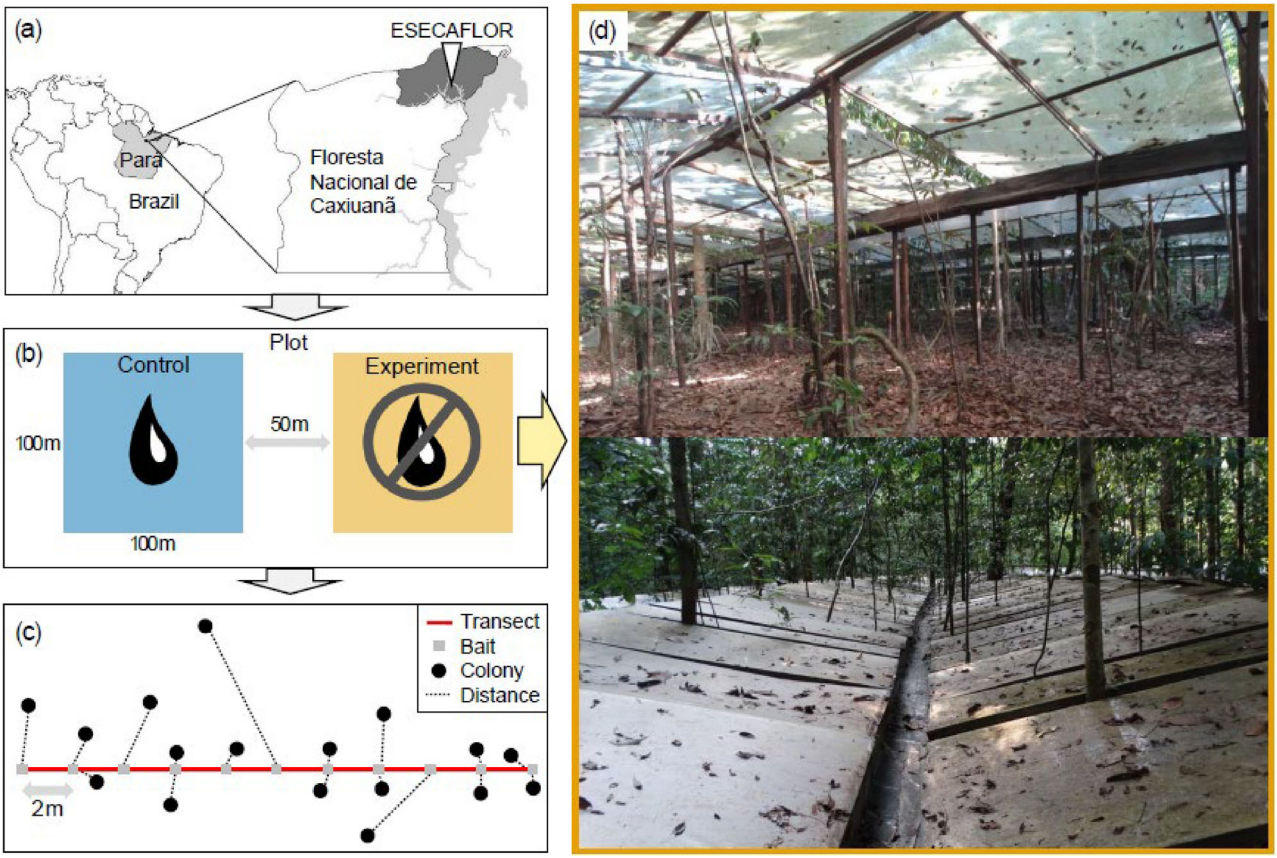

FIGURE 1 (a) Location of the ESECAFLOR experiment in the Floresta Nacional de Caxiuanã, Pará, Brazil; (b) control (blue) and experimental (yellow) plots. The experimental plot contains (d) plastic panels to exclude ≈50% of precipitable water from the system (photo below and above the panels, respectively). (c) Experimental design in both plots with the transect (continuous red line), baits (grey squares), examples of colonies (black circles), and the straight-line distance between the bait and ant nests (black dotted line).

14–17 h, and at least 2 h after rain so as to avoid its short-term effects on ant activity (Kaspari & Weiser, 2000). At each sampling date, baits were placed every 2 m along five 20-m-long linear transects randomly arranged within each plot (11 baits per transect; Figure 1c). An individual bait station consisted of ≈3 g of a mixture of canned sardines and manioc flour in equal proportions, placed on a small piece of paper (10 × 10 cm; Figure S1) atop the litter. After 10 minutes, all ants that were seen foraging at each bait were followed back to their nest entrance, which was flagged and marked with a unique identifier (Figure S1). The search effort for the colonies was standardised to 60 minutes and three people per transect, where each observer monitored three to four baits (Figure S1). After the search time, we measured the detection distances as the linear distance between the bait and nest (Figure 1c).

Specimens from all baits were collected and fixed in 70% alcohol. To ensure the association between the ants, resources, and the particular location of the colony, whenever possible we collected individuals on baits, foraging trails, and inside the nest (Baccaro & Ferraz, 2013). We also collected different castes for dimorphic (*Pheidole*) or polymorphic (*Solenopsis*) species to ensure we had an adequate range of intraspecific morphological variation to ensure accurate species-level identification. Specimens were identified to species or morphospecies using (i) specialised taxonomic keys (Feitosa & Dias, 2024; Wilson, 2003); (ii) reference material from other collections made at ESECAFLOR (Almeida, Silva, et al., 2023); (iii) consultation with specialists; and (iv) through comparisons with the reference collection in the Entomological Collection of the Museu Paraense Emílio Goeldi (MPEG), where all collected specimens were deposited after the species identification process.

Statistical analyses

We performed all analyses in the R software system (version 4.1.0; R Core Team, 2021). Figures were created using the *ggplot2* (Wickham, 2016), *gridExtra* (Auguie, 2017), and *ggrepel* (Slowikowski, 2020) packages.

Induced drought effect on the generalist ant assemblage

We tested assemblage-wide effects of induced drought using transects as sampling units ($N = 20$). Plot (control or experimental) was

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the predictor variable, and species richness, abundance of colonies, and species composition were the response variables. We tested plot effects on species richness and abundance of colonies using generalised linear model (GLMs) with Poisson or Negative binomial errors (Table S1). We used the "gofstat" function from the *fitdistrplus* (Delignette-Muller & Dutang, 2015) package to calculate the goodness-of-fit statistics for the different error distributions (Poisson and Negative binomial). Then, we selected the better model distribution based on the AIC (Akaike Information Criterion) to create GLMs models. GLMs were constructed using the "gamlss" function of the *gamlss* (Rigby & Stasinopoulos, 2005) package.

We tested whether species composition differed between plots using a permutational multivariate analysis of variance (PERMANOVA; Clarke, 1993) as implemented in the "adonis2" function in the *vegan* R package (Oksanen et al., 2019) with 9999 randomisations. We used principal coordinates analysis (PCoA) to visualise species composition using the "cmdscale" function of the *vegan* R package. Assemblage abundance for PCoA and PERMANOVA was defined as the number of colonies; we used the Bray–Curtis index in the distance matrix (Gotelli et al., 2011).

Finally, we used a multinomial species classification method (CLAM; Chazdon et al., 2011) to classify species into three ecological groups: (i) indicators of the undisturbed forest (control); (ii) indicators of forests undergoing drought (experiment); and (iii) distribution independent of habitat (i.e., occurs in both plots). We used the "clamtest" function in the *vegan* package with a simple majority threshold value (K = 1/2).

Induced drought and ant detection distance

We investigated the effect of induced drought on bait detection distance (defined as the linear distance from the bait to the nest) at three scales: (i) within transects; (ii) among species; and (iii) within species. This approach allowed us to control for and better understand species-level features, such as foraging areas (Byrne, 1994). In Amazonian forests, some ant colonies can detect and transport resources over distances longer than 4 m (Baccaro & Ferraz, 2013); thus, in our sampling design, a given colony that foraged for distances >1 m could detect more than one bait at the same time. In cases where the same colony was detected more than one bait, we kept only the longest detection distance in our data set to avoid pseudoreplication. Besides that, we did not use the number of nests as a variable in the models, as we did not detect a correlation between the number of ant colonies and the average foraging distance (Figure S2).

At the transect scale, we compared the median bait detection per transect between plots (control and experimental) using a generalised linear model (GLM). The sample unit was the transect ($N = 20$), the median detection distance was the response variable, and the plot (control or experimental) was the predictor.

We tested drought effects among species in two ways. First, we compared the median detection distances of the six most common species (i.e., ≥ 4 records by plot) found in both the control and the experimental plots using a paired *t*-test (i.e., six median values by plot; $N = 12$) with the "t.test" function in the *stats* R package (R Core Team, 2021). Second, we used the species selected in CLAM and tested for differences among the median detection distances of the species between the three ecological groups using a GLM.

Last, we investigated the drought effects within these same six most common species. For this, we compared the detection distance between colonies of the same species recorded in the undisturbed (control) forest and the drought-induced (experimental) forest. We analysed species individually, using the distance of colonies as a response variable in a GLM model (i.e., six GLM models).

The GLMs were fitted based on maximum likelihood estimation (Table S1), with residual errors following Lognormal, Gamma, or Weibull distributions (Pringle et al., 2019). Then, we used the best-fitting GLM model using the AIC. The lognormal distribution correctly describes the center of the empirical distribution, but the Weibull or Gamma distributions could be preferred for their better fit to the right tail of the distribution (i.e., skewed to the right; (Delignette-Muller & Dutang, 2015), as it is in the context distance detection of resources by ants). We also used the *fitdistrplus* R package (Delignette-Muller & Dutang, 2015) to fit the statistical error distribution and *gamlss* R package (Rigby & Stasinopoulos, 2005) to build the GLMs.

RESULTS

General patterns

In total, we recorded 312 colonies of 63 ant species across the control and experimental plots. We recorded 208 colonies of 54 ant species in the control plot and 104 colonies from 31 species in the experimental plot; 22 ant species were recorded in both plots (Table S2). *Pheidole* had the highest number of species (28 spp., 44%) and colonies (178 colonies, 57%). The species with the highest numbers of colonies recorded were *Pheidole fracticeps* Wilson, 2003, *P. biconstricta* Mayr, 1870 and *Crematogaster levior* Longino, 2003 with 31, 23, and 22 colonies, respectively (Table 1). The resource detection distance ranged from 7 cm (*P. fracticeps* and *Solenopsis* MPEG 07) to 70 m (*Neoponera verenae* Forel, 1922). The median resource detection distance in the control plot was 46 cm (range = 7–7000 cm) and 54 cm (range = 7–695 cm) in the experimental plot. We recorded 29 (9%) ant colonies (i.e., the same colony) visiting two or three baits along the transect.

Induced drought and the response of the generalist ant assemblage

Regarding our first hypothesis, we found that induced drought modified the assemblage of generalist ants by reducing the number of colonies, reducing the number of species, and modifying their species composition. The control plot had twice as many colonies as the drought-induced plot ($t_{1,18} = -5.8$; $p < 0.001$; Figure 2a). The species

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TABLE 1 Classification of the most commonly recorded ant species (≥4 records per plot) sampled in the control and experiment plots in ESECAFLOR.

Species	Code	N° nest[a]	Distance (cm)[b]	CLAM
Crematogaster levior	Cr.lev	22 (7 + 15)	79.60 ± 75.54	Experiment
Mayaponera constricta	Ma.con	10 (1 + 9)	57.56 ± 33.82	Experiment
Paratrachymyrmex nr. *bugnioni*	Pa.bug	12 (7 + 5)	29.70 ± 20.03	Generalist
Pheidole astur	Ph.ast	7 (2 + 5)	119.00 ± 59.09	Experiment
Pheidole biconstricta	Ph.bic	23 (21 + 2)	309.90 ± 254.29	Control
Pheidole cursor	Ph. cur	21 (17 + 4)	73.10 ± 35.65	Control
Pheidole fracticeps	Ph. fra	31 (22 + 9)	23.80 ± 14.14	Generalist
Pheidole jeannei	Ph.jea	16 (15 + 1)	83.00 ± 88.70	Control
Pheidole pygmaea	Ph.pyg	9 (6 + 3)	14.10 ± 3.80	Generalist
Pheidole schwarzmaieri	Ph.sch	8 (4 + 4)	38.00 ± 20.22	Generalist
Pheidole scolioceps	Ph.sco	8 (4 + 4)	25.05 ± 9.71	Generalist
Pheidole triconstricta	Ph.tri	10 (0 + 10)	138.70 ± 82.95	Experiment
Wasmannia auropunctata	Wa.aur	8 (2 + 6)	38.16 ± 33.67	Experiment

Abbreviations: CLAM, Multinomial Species Classification Method; Control, associated with control plot; Experiment, associated with experimental [drought-induced] plot; Generalist, generalists between plots.
[a]Number total of colonies (Control + Experiment);
[b]Median ± SD.

richness recorded in the control plot was also approximately twice that in the drought-induced plot ($t_{1,18} = -4.0$; $p < 0.001$; Figure 2b). Finally, species composition differed between the plots (Pseudo-$F_{1,18} = 3.7$; $r^2 = 0.172$; $p < 0.001$), and the PCoA explained 36% of the total variation on the first two axes (Figure 2c). Of the 63 recorded species in our study, the CLAM classified three species as control plot indicators (5%), five as plot-independent (8%), and five as drought plot indicators (8%; Table 1). The remaining species (50; 80%) had frequencies too low to be reliably classified into any ecological group (Figure 3; Table S2).

Induced drought and resource detection distance

Regarding our second hypothesis, we found that resource detection distances in the control and the induced-drought plots were similar at the transect scale (Table 2; Figure 4a). We also did not find differences among (Figure 4b) or within (Figure 5) the six most common species in resource detection distances (Figure 4b). However, we did find differences among groups of ants: species associated with only one of the control or induced-drought plots had greater foraging distances than species that nested in both environments (Table 2; Figure 4c).

DISCUSSION

We quantified the effects of an experimentally induced drought on ant species richness and nest abundance, and tested whether such changes translated into differences in foraging distances of generalist ants in a primary Amazon rainforest. Drought caused a 50% reduction in species richness and colony abundance and substantial changes in the species composition of the generalist ant guild. However, we did not find differences in foraging distances to surface resources when precipitable water availability was experimentally reduced, either for individual species or for the entire ant assemblage. Ant species associated with both control and drought-induced forest plots foraged for shorter distances than the species associated with only one plot type (i.e., control or drought-induced plots).

Induced drought reduces the richness and number of colonies and modifies the composition of foraging generalist ant species

Our results are consistent with previous studies assessing the impact of drought on ant diversity in tropical forests (e.g., Almeida, Silva, et al., 2023; Delsinne et al., 2013; Ribeiro-Neto et al., 2023). However, although the reduction in species richness and colony density caused by drought is one of the most severe effects on the ant fauna (Parr & Bishop, 2022), it was not responsible for marked changes in resource removal from the soil surface of tropical forests. One reason for this lack of pattern may be the extremely high number of ant species in tropical forests; in a previous study assessing total ant diversity in the same experiment, we found more species in the control plot (172 spp.), but still a relatively high number of species in the plot subject to induced drought (157 spp.) (Almeida, Silva, et al., 2023). Even among the subset of generalist feeding ants, we still found a relatively high number of foraging ants in the drought-induced treatment (31 spp.). We also found striking differences in ant species

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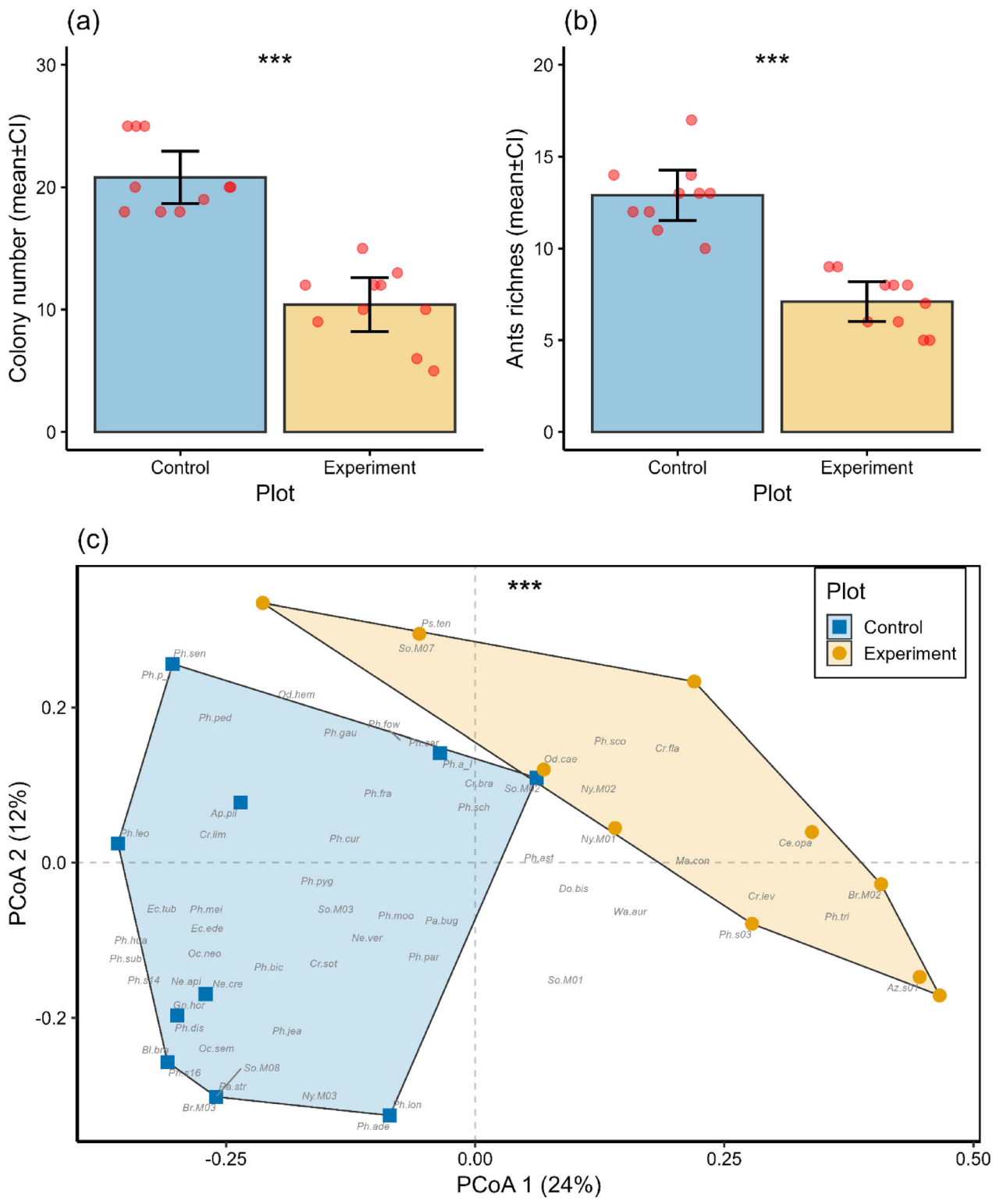

FIGURE 2 The (a) number of colonies, (b) richness species, and (c) composition (PCoA) of ants collected in the ESECAFLOR plots (control and experiment). ***p < 0.001. The red points represent the transects. CI, 95% confidence interval. See Table S2 for species codes (b).

composition between the two treatments. The combination of the previous results with the ones from this study gives us clear indications of the role of high diversity patterns in shaping the observed differences between the plots. Notably, generalist ant species could easily replace other species, simply by occupying the niches of species formerly found in a given habitat. As generalist ant species may benefit from more open and drier habitats (Andersen, 2019), they may also replace those species with narrower niches, which may go locally extinct because of changes in specific conditions and in the availability of specific feeding and nesting resources (Parr & Bishop, 2022).

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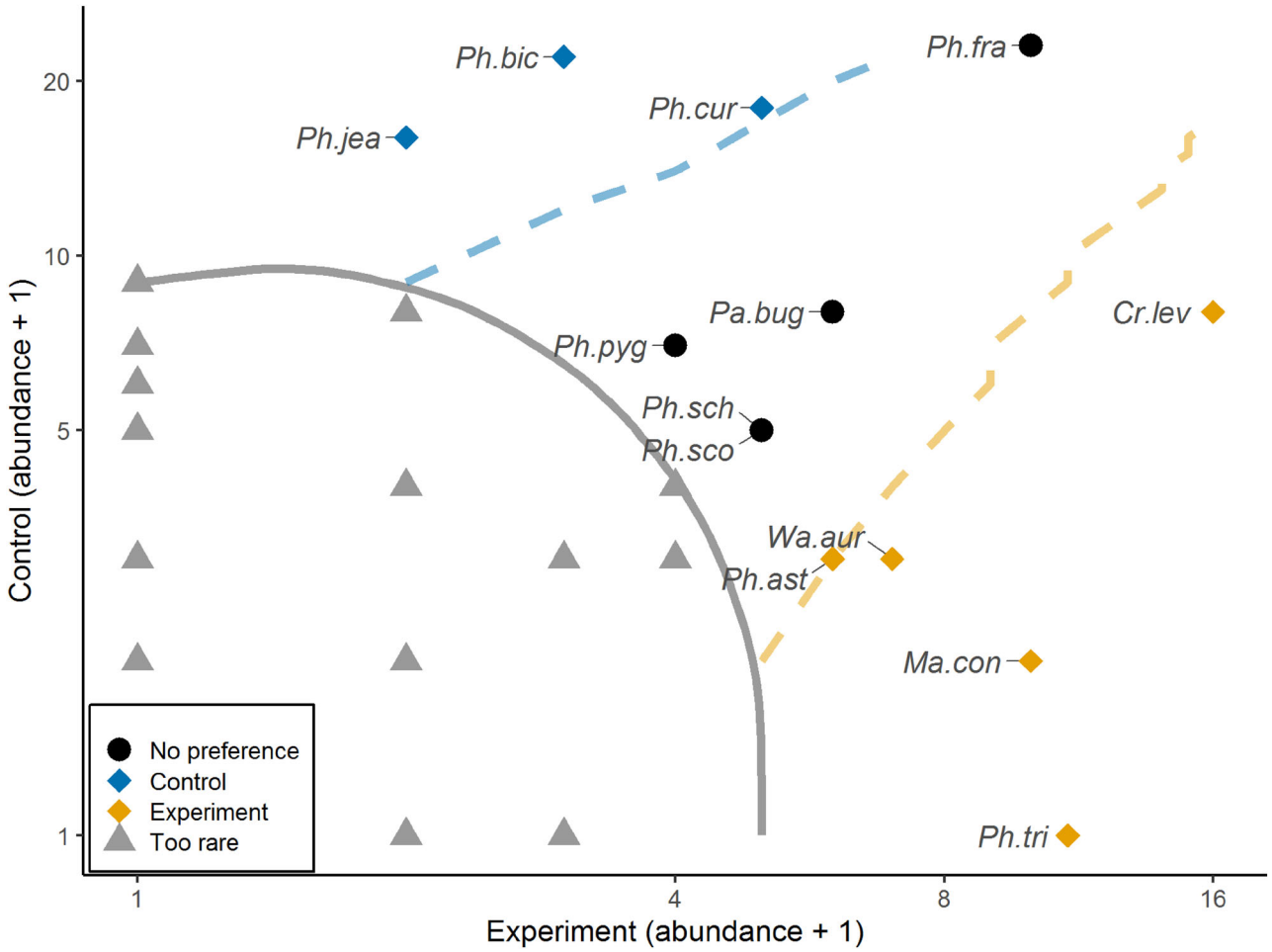

FIGURE 3 CLAM analysis classifying the 63 species of ants into four classes according to their frequency of occurrence in the plots: Associated with the control plot (natural area; blue diamond in colour version: *Pheidole cursor*; *Pheidole biconstricta*; and *Pheidole jeannei*); no association with control or experimental plots (black circles: *Paratrachymyrmex* nr. *bugnioni*; *Pheidole fracticeps*; *Pheidole pygmaea*; *Pheidole schwarzmaieri*; and *Pheidole scolioceps*); associated with the experiment plot (induced water exclusion; yellow diamond in the colour version: *Crematogaster levior*; *Mayaponera constricta*; *Pheidole astur*; *Pheidole triconstricta*; and *Wasmannia auropunctata*); and too rare to be assigned specificity preference (grey triangle).

TABLE 2 Model results for comparisons between the detection distance of baits in the control and experimental plots, using different response levels for ants collected in the induced drought experiment.

Response variable	Predictor variable	Scale	Sampling unit	Error-distribution family	*t*	*P*	df
Median distance	Plot	Transect	Transect	Weibull	1.484	0.156	1, 18
Median distance	Plot	Among-species	Species	Gaussian	−0.925	0.397	6, 5
Median distance	Groups (CLAM)	Among-species	Species	Lognormal	4.695	**0.001**	2, 10
Colony distance	Plot	Within-species	Colony (Cr.lev)	Lognormal	1.467	0.159	1, 20
Colony distance	Plot	Within-species	Colony (Pa.bug)	Lognormal	0.148	0.886	1, 10
Colony distance	Plot	Within-species	Colony (Ph. cur)	Weibull	−1.126	0.275	1, 19
Colony distance	Plot	Within-species	Colony (Ph. fra)	Lognormal	0.058	0.955	1, 29
Colony distance	Plot	Within-species	Colony (Ph.sch)	Weibull	2.554	0.051	1, 6
Colony distance	Plot	Within-species	Colony (Ph. sco)	Weibull	2.348	0.066	1, 6

Note: See Table 1 for species codes; df, degrees of freedom in numerator and denominator. Bold values are significant values.

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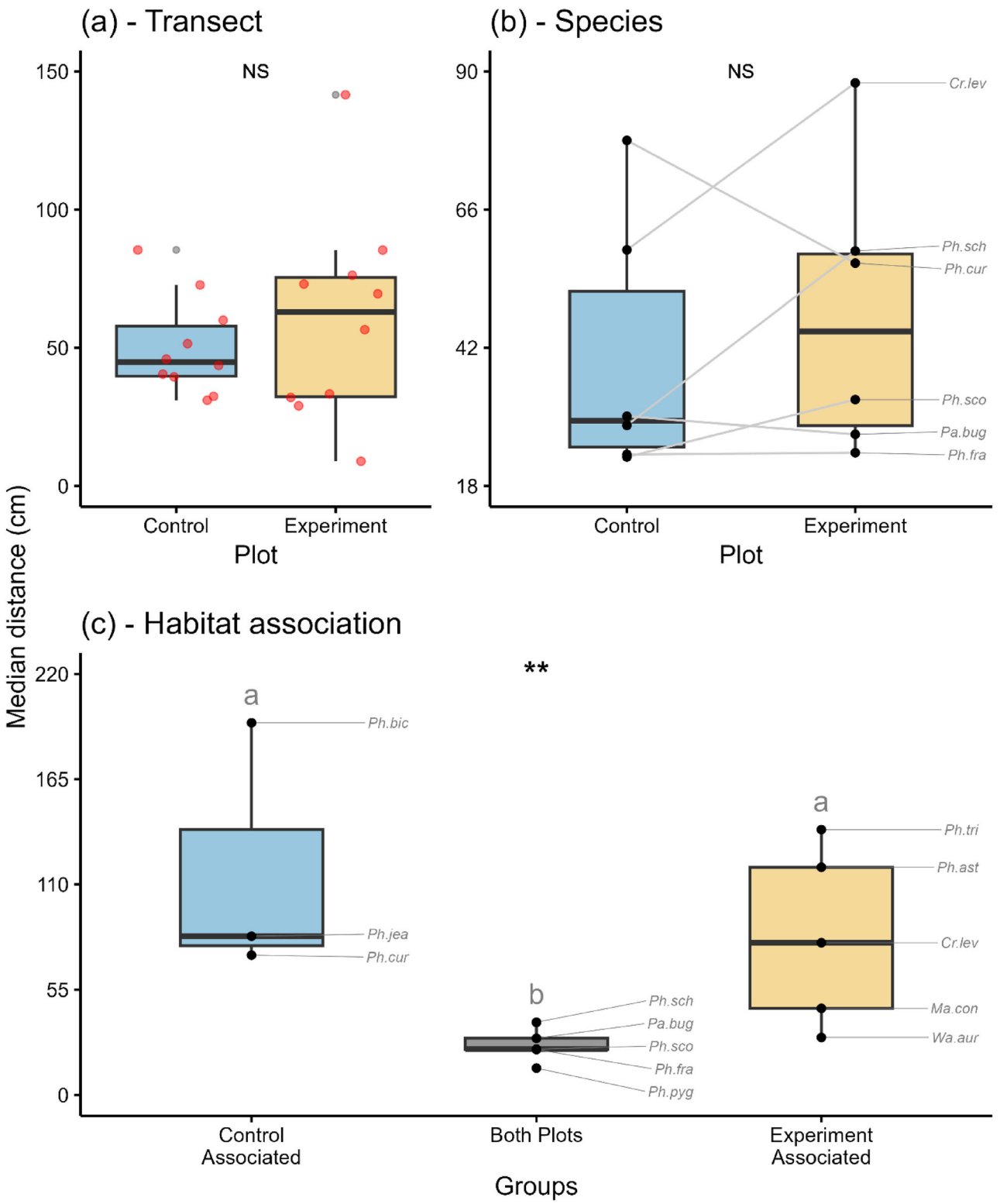

FIGURE 4 Detection distance of baits by ants as a function of (a) transects, (b) most commonly recorded species (≥4 records by plot) in the control and experimental plots, (c) habitat association classified using a CLAM analysis (associated only with the control plot, associated with both plots, associated only with the experimental plot) for ants collected in an induced drought experiment. The red points represent the median of the distances of the colonies of each transect (a), and the black points represent the median of the distances of the colonies for each species (b and c). *p value*: NS >0.05; ** < 0.01; see Table 1 for species codes; different letters represent significant differences in (c).

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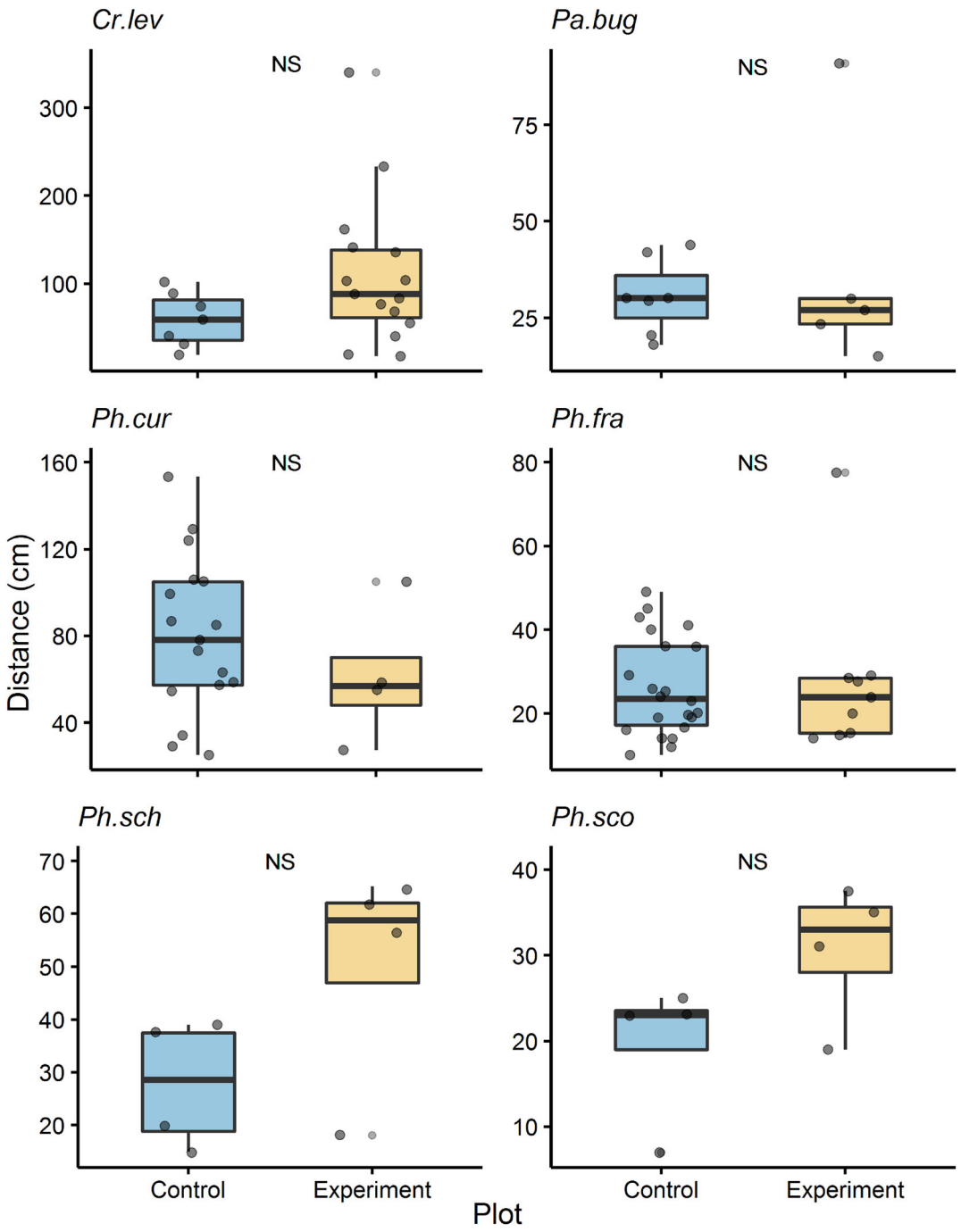

FIGURE 5 Resource detection distance of the most frequent species found (≥4 records by plot) in the ESECAFLOR plots (control and experimental). The black points represent the colonies of each species. NS: $p > 0.05$; see Table 1 for species codes.

If the rate of climate change increases, however, even the high diversity of tropical forest ants might not be sufficient to prevent the effects of forest drought on ant community composition (Parr & Bishop, 2022). Although we studied a guild of generalist ants, we found that 87% of the species recorded had less than ten colonies in a primary tropical forest. We suggest that these generalist species should be considered carefully in future studies as they are associated with ecosystem processes and are essential for understanding species coexistence (Pearce-Duvet et al., 2011; Walker et al., 2024).

Induced drought does not influence resource detection distance by generalist ants

Rainfall is positively related to the diversity of items available to and consumed by ants (Anjos et al., 2019; Lasmar et al., 2021). However, drought had no apparent effect on the distance at which ants detected resources among transects, between species, or within species. We expected that colonies of a given species would show a decrease in resource detection distance because environmental stress

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caused by drought negatively affects ant activity (Kaspari & Weiser, 2000; Parr & Bishop, 2022). Indeed, we found clear indications that although species composition changed with experimental drought (some species went locally extinct and others arrived), the arriving species had a similar foraging distance as the ones that went locally extinct. In addition, it is true that, as occurs with temperature (e.g., Jayatilaka et al., 2011; Stuble et al., 2013), different ant species might have different physiological limitation to foraging in distinct ranges of drought conditions. However, if this variation is solely related to temperature constraints, then we would expect that the same species occurring in dry and wet habitats should display very different foraging distances. This was not the case for the common species that occurred in both the experimental and control treatments, especially the habitat specialists (Figures 4b and 5).

However, we found evidence that habitat-generalist species (i.e., species with colonies in both the undisturbed and drought-induced plots) had shorter foraging distances in the drought-induced plot. Shorter foraging distances have implications for certain services, such as seed dispersal. Furthermore, ant species classified as habitat-specific in our study (undisturbed vs. drought-associated species) did not differ in their foraging distances, suggesting that species turnover between drought and control assemblages was driven by species with similar foraging distances. The absence of species with narrower survival thresholds (i.e., species found only in undisturbed forests) may facilitate the presence and dominance of thermophilic species (Baccaro et al., 2013; Diamond et al., 2016; Roeder et al., 2021) that can also detect food resources over long distances. Thus, species replacement or increases in colony density of ants in a drier forest may favour the detection of resources on the ground and maintain resource removal.

CONCLUSION

We found strong negative effects of drought in the diversity of generalist foraging ants in a unique experimental forest. Nevertheless, such effects did not translate into differences in foraging distances between the experimental treatments, either for individual species or for the entire ant assemblage. Our results illustrate the complex dynamics of species replacement in tropical rainforests of the western Amazon, which has an extremely rich ant fauna and that is particularly vulnerable to global warming (Parr & Bishop, 2022). Although our study is an essential step in understanding the effects of forest drought on ant foraging patterns, many issues remain to be addressed. First, our baits consisted of generic food items, but it is well known that resource demand can vary according to environmental constraints that may limit the available resource pool (e.g., Lasmar et al., 2021). Indeed, ants tend to be more attracted to baits that offer less-common resources in a particular habitat (e.g., forest or grassland) and microhabitat (e.g., litter or canopy). Second, studies focusing on specialised foraging guilds (e.g., predatory ants) may reveal different effects of drought from those observed for generalist guilds of species. Finally, tropical forests have highly compartmentalised stratified ant faunas (e.g., soil-litter-vegetation) (Almeida, Teresa, et al., 2023), and ants from different strata can respond differently to shifts in climatic conditions (Parr & Bishop, 2022). Thus, future studies also need to consider the potential role of ant stratification in shaping responses to increased desiccation.

AUTHOR CONTRIBUTIONS

Rony P. S. Almeida: Conceptualization; formal analysis; data curation; methodology; investigation; project administration; validation; visualization; writing – original draft. **Fabrício B. Baccaro:** Investigation; writing – review and editing. **Aaron M. Ellison:** Conceptualization; investigation; methodology. **Flávio Camarota:** Investigation; writing – review and editing. **Rogério R. Silva:** Funding acquisition; investigation; writing – review and editing; resources; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicting interests to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in harvard forest at https://harvardforest1.fas.harvard.edu/exist/apps/datasets/showData.html?id=HF351.

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