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HIGHLIGHTED STUDENT RESEARCH

Induced drought strongly affects richness and composition of ground-dwelling ants in the eastern Amazon

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Abstract

Species loss in tropical regions is forecast to occur under environmental change scenarios of low precipitation. One of the main questions is how drought will affect invertebrates, a key group for ecosystem functioning. We use 1 year of data from a long-term rainwater exclusion experiment in primary Amazonian rainforest to test whether induced water stress and covarying changes in soil moisture, soil respiration, and tree species richness, diversity, size, and total biomass affected species richness and composition (relative abundance) of ground-dwelling ants. Data on ant abundance and environmental variables were collected at two sites (control and experimental) in the Eastern Amazon. Since 2002, drought has been induced in the experimental plot by excluding 50% of normal rainfall. Ant species richness in the experiment plot was reduced and some generalist species responded positively. Ant species richness also increased in the experimental plot with increasing diversity of the plant species of the leaf litter. The relative abundance of ants differed between plots. The experimental plot was characterized by a higher frequency of generalist and other species that appeared to be favored by the reduction in rainfall. Between-plot comparisons suggested loss and changes in ant species composition in tropical forests were affected by increasing dryness. These changes could ultimately lead to cascading effects on ecosystem processes and the services they mediate.

Keywords Amazonia · Climatic change · Formicidae · Tropical rainforest · Water stress

Introduction

Different scenarios of climatic change for the Amazon Basin include changes in temperature, precipitation, and relative humidity (Phillips et al. 1979; Davidson et al. 2012; Mora et al. 2013; Costa et al. 2020). The majority of these scenarios forecast a long-term reduction in rainfall for ≈50% of Amazonia, leading to widespread droughts (Marengo et al. 2018). Global models also forecast insect species losses ranging from 6% with 1.5 °C warming to 49% with ~ 3.2 °C warming by the year 2100 (Warren et al. 2018), but the effects of drought on invertebrate biodiversity are virtually unknown (Ruivo et al. 2007; Diamond et al. 2012; Baccaro et al. 2013; Sánchez-Bayo and Wyckhuys 2019). Drought reduces photosynthesis and causes hydraulic imbalances that

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We highlight ground-dwelling ants community structure in a long-term experiment with the exclusion of water rainfall in the Amazon. Our conclusions illustrate effects of drought on invertebrates.

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tend to kill larger trees (Meir et al. 2015, 2018; Costa et al. 2017; Olson et al. 2018). The associated loss of biomass and plant litter input will alter soil microclimate, which may reduce or eliminate foraging and nesting sites for ground-dwelling invertebrates (Byrne 1994; Fernandes et al. 2019). Loss of invertebrate species also will alter ecosystem processes and functions (Coyle et al. 2017), including reduction of organic matter decomposition and nutrient cycling rates and retention of soil humidity (Griffiths et al. 2018).

Ants interact with many plants and animals, are important components of most terrestrial ecosystems (Schultheiss et al. 2022), and provide key ecological services in most ecosystems (Andersen 1997; Elizalde et al. 2020). Changes in rainfall should strongly affect ants by altering environmental conditions crucial for their survivorship and changing the availability of food and habitat resources that further affect their fitness (Baccaro et al. 2013; Silva and Brandão 2014). For example, ants and other invertebrates inhabiting tropical forests are likely to be physiologically more sensitive to climatic change because they already experience temperatures closer to their thermal tolerance limits than do these same species living in temperate environments (Diamond et al. 2016; Warren et al. 2018). In line with this hypothesis, large ant species (e.g., *Dinoponera quadriceps*) in tropical dry forest disperse fewer seeds as rainfall declines (Oliveira et al. 2019). In tropical wet forests, some ant species (e.g., *Pheidole nigricula*) do not change foraging activity as temperature increases, but abundance of their invertebrate prey may decline with changing temperatures, with cascading negative consequences for ant species richness and abundance (Byrne 1994; Coyle et al. 2017).

Changes in rainfall regime in tropical forests also have scale-dependent effects on ant assemblages. For example, the east–west continental gradient in rainfall distribution in Amazon (Silva et al. 2019) is associated with ant species richness along the Amazon River (Vasconcelos et al. 2010). Areas in the Amazon where the water table is often deeper throughout the year have fewer, small-size hypogaeic foragers and Dacetini predators but more species of generalist ants (Baccaro et al. 2013). In drier "edge" habitats in the Amazon, there is a strong dry season influence in the ant species composition and increased richness because of the occurrence in these edges of thermophilic species of nearby open areas or canopy specialists (Arruda et al. 2021). Finally, a short-term (6 month), small-scale (3 × 3 m) rainfall exclusion experiment altered the relative abundance of several ant species but did not change overall ant species richness (Delsinne et al. 2013).

Our study compares the ground-dwelling ants in a rainwater exclusion experiment (henceforth "induced drought") in an area of the Amazon rainforest. Our predictions are that induced drought (i) reduces ant species richness; and (ii) changes patterns of relative abundance (species composition) by favoring species associated with habitat alteration. Finally, (iii) we predicted an increase in occurrences of generalist ants in the experimental plot in which drought was induced. Our predictions are linked to changes in temperature, humidity, and habitat structure—key determinants of ant success (Kaspari and Weiser 2000; Kaspari et al. 2010)—because induced drought has been shown to lead to changes in both habitat structure (Coyle et al. 2017; Fernandes et al. 2019) and soil microclimate (Baccaro et al. 2013; Diamond et al. 2016).

Materials and methods

Study area

The "Effects of Forest Drought" experiment (ESECAFLOR) is a large-scale, long-term rainfall exclusion experiment established in 2001 to study impacts of sustained low water supply (induced drought) on local microclimate, vegetation, and ecosystem processes in a *terra firme* rainforest (Meir et al. 2018). ESECAFLOR is located at the Ferreira Penna Scientific Station (ECFPn) in the Caxiuanã National Forest (FLONA), Pará, Brazil (1.718° S, 51.46° W). Average air temperature at ECFPn ≈ 26 °C and daily variation in temperature < 4 °C (Ruivo et al. 2007). The soils in this *terra firme* forest are yellow oxisols, 10–15 m above river level. Average annual precipitation is 2000–2500 mm but < 100 mm/month falls during the dry season, which runs from June to November (Ruivo and Cunha 2003).

ESECAFLOR includes a pair of 1-ha (100 × 100 m) plots. In January 2002, transparent plastic panels were installed 2 m above the soil in one of the plots (the experimental plot) to exclude ≈ 50% of precipitable water (Fig. 1a). All water collected by the panels is directed to a gutter and dispensed 50 m outside the experiment and this reduction is similar to the long-term forecast for the region (Marengo et al. 2018). Ninety-five percent of incident light is transmitted through the transparent panels, ensuring that they do not alter luminosity at the forest. However, increased tree mortality in the experimental (drought-inducing) led to increased aboveground light levels because of loss of the upper tree canopy (Ferreira et al. 2016). Panels are maintained regularly; plastic and panel structures are repaired immediately when they are damaged by falling branches. Plant litter that accumulates on the panels is removed weekly and spread evenly on the ground below each panel. The second, control plot is located 50 m away from the experimental plot. The topography, soil type, and vegetation structure are similar in both plots (Fisher et al. 2007; Meir et al. 2018). Detailed information on the experimental set-up of ESECAFLOR was published in Costa et al. (2010); Rowland et al. (2015).

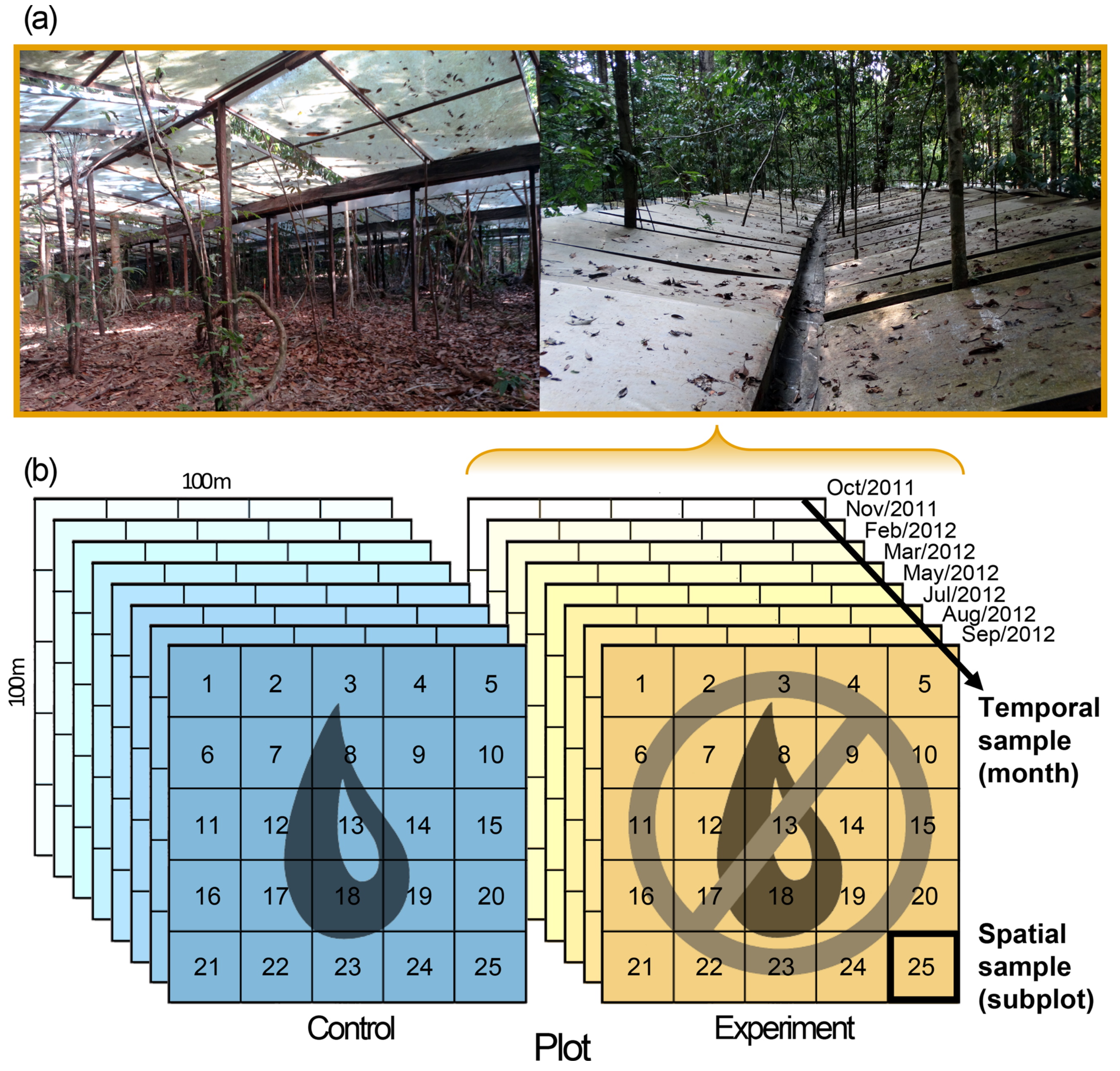

Fig. 1 **a** Photos obtained from below (left) and above (right) of the plastic panels that exclude rainwater at the experimental plot. **b** Experimental design for both plots (control and experimental), illustrating the temporal (months) and space (subplots) samples for collecting ants and environmental data, in ESECAFLOR, Ferreira Penna Scientific Station (ECFPn), Caxiuanã National Forest (FLONA), Pará, Brazil

The ESECAFLOR project is located in a remote area of primary rainforest in the Amazon Basin. As is often the case in large-scale manipulative studies, the ESECAFLOR has some limitations, most notably the fact that it is the only large experiment at the site and the experimental treatment, although large in spatial experiment (1 ha), is unreplicated. As with analysis of forest dynamics plots, our statistical inferences and conclusions apply only to the single site, but we note for scale that a 1-ha plot seen by a 5-mm-long ant is comparable to a 4 km^2 area seen by a 2-m-tall human. Furthermore, our experimental design is a Control-Impact (CI) design, not a Before-After Control-Impact (BACI). Although a BACI design would have been the ideal approach for such an unreplicated experiment (Christie et al. 2019), pre-treatment data were not collected. Rather, the experimental and control plots were established on a site which had been found to have comparable soil and vegetation structure across the two plots before the experimental infrastructure was installed (Fisher et al. 2007; Costa et al. 2010; Rowland et al. 2015; Ferreira et al. 2016; Meir et al. 2018).

Ant sampling

We studied processes and mechanisms that affect the ants in the experiment by subdividing each 1-ha plot (induced drought, control) into smaller, 20 × 20 m subplots and over a year of sampling—a 'spatial' and 'temporal' model, respectively (Fig. 1b). Similar subplotting and associated analyses are done routinely throughout the world across the broad network of large, unreplicated tropical forest dynamics plots (Anderson-Teixeira et al. 2015). Subplots were considered to be spatially independent, because these 400 m^2 subplots are at least two orders of magnitude larger than the foraging area of most tropical ant species: 66% of the foraging area for a given ant nest in tropical wet forests < 1 m^2 (Baccaro and Ferraz 2013). Ants were sampled using pitfall traps—an efficient method for collecting ground-dwelling ants in the Amazon (Souza et al. 2012)—in all subplots in October and November 2011 and again in February, March, May, July, August and September 2012 (Fig. 1b). For pitfall traps, we used 500 mL cups (10 cm diameter) containing water, salt, and a few drops of detergent. The cups were covered to avoid overflow from rains and to avoid trapping larger arthropods and small vertebrates (Bestelmeyer et al. 2000). We placed four pitfall traps in each subplot in each month (total sampling effort = 1600 pitfall traps). Traps were left open in the field for 48 h. Accumulated ants were then transferred into vials containing 80% ethanol; individuals from each species in each sample were mounted and identified. Voucher specimens were deposited in the Entomological Collection of the Museu Paraense Emílio Goeldi, Belém, Brazil.

Environmental variables

The ESECAFLOR experiment monitors variables that describe the dynamics of the local environment (solar radiation/min, air temperature and humidity at 1 and 10 m above ground/min, ground temperature and humidity at 5-, 10- and 50-cm depth/min, precipitation/hour) and vegetation composition. We tested the relationship between ant species composition (richness and abundance) and the effects of induced drought using a set of variables related to food resources and diversity of microhabitats for ants, their foraging opportunities, and nesting sites (Supporting Information, Figs S1) (Byrne 1994; Armbrecht and Perfecto 1979; Kaspari et al. 2010; Vasconcelos et al. 2010; Jenkins et al. 2011; Delsinne et al. 2013; Diamond et al. 2016; Bujan et al. 2016; Coyle et al. 2017; Guilherme et al. 2021). We used as covariates in our analysis those variables that matched both the period of our ant sampling (temporal data; three covariates) and the spatial data (six covariates) in the 20 × 20-m plots (Table 1). Additional information on data acquisition and data ranges at ESECAFLOR is in the Supporting Information.

Data analysis

We analyzed the effects of drought-related changes in the forest environment and vegetation on ant species richness and relative abundance in both space and time. For the "spatial model", the 20 × 20 m subplots were considered as the sampling units (Fig. 1b; all data pooled over time). Although subplots are not independent with respect to treatment (Hurlbert 1984), treating subplots as independent spatial replicates was justified here because there was no spatial autocorrelation in the values of species richness among subplots within each 1-ha ESECAFLOR plot (control plot: Moran's $I = 0.035$, $P = 0.41$; experimental plot: Moran's $I = 0.085$; $P = 0.93$). For the "temporal model", months were considered as the sampling units (Fig. 1b; all data in each of the two ESECAFLOR 1-ha plots pooled for each month). There was no collinearity among predictors in either the spatial or temporal models for combined and separated data (Supporting Information, Figs S2 and S3 for combined data).

To test for experimental effects on species richness in both the spatial and temporal models, we used generalized linear mixed models (GLMMs) implemented in the "lme" function of the *nlme* package (Pinheiro et al. 2020) in the R software system (version 4.1.2, R Core Team 2021). To understand the relationship between ant richness and environmental variables at the subplot scale (spatial model) or over time (i.e., months, the temporal model), we used a model containing each variable and an interaction term between variables and the experimental plot (control or induced drought). Plot type entered the model as a random term, because the sampling units (subplots or months) were sub-samples of each plot. Model selection was done using AICc values (Burnham and Anderson 2002) computed with the "dredge" function of the *MuMIn* package (Barton 2020). Model variables were included when their importance factors > 0.7 (on a 0–1 scale) based on their occurrence in the selected feasible models (Burnham and Anderson 2002). To evaluate the effect of induced drought alone on ant richness, we also used *t*-tests for both models; for the spatial model we used an unpaired *t*-test, but for the temporal model (month), we used a paired *t*-test.

To test whether ant species composition (relative abundances) differed between treatments, we used Permutational Multivariate Analysis of Variance (PERMANOVA; Clarke 1993) as implemented in the "adonis" function in the *vegan* package (Oksanen et al. 2020) with 9999 randomizations. Ant composition was our response variable, and the environmental variables in space (subplot) or time (months), and plot (control and induced drought) were used as explanatory variables. Analyses were included in the models by order

Table 1 Covariates selected for analyses of ant data in ESECAFLOR experiment, sample scale (temporal and spatial), and data dimension

Predictor	Samples	Description and effects on ants	Data extent
Moisture	Spatial and temporal	Soil moisture collected by the meteorological tower and manually in each plot. Measured in %. Reduction in soil moisture reduces resource diversity for specialist ants (Baccaro et al. 2013) and affects conditions for desiccation-sensitive species (Bujan et al. 2016)	50 Subplots totaling 400 measures; 8 months totaling 23,424 measures
Litter diversity	Spatial and temporal	Components of litter biomass (measured in grams: leaves, twigs, flowers, fruits, and miscellaneous) submitted Hill number in order 1. Reduced litter diversity affects species that use specific items such as twigs for nesting (Byrne 1994; Fernandes et al. 2019)	50 Subplots × 5 components × 8 months totaling 2,000 measures
Litter biomass	Spatial and temporal	Sum of all litter biomass items. Measured in grams. Litter biomass reduction affects species that use this substrate for nesting and foraging (Byrne 1994; Queiroz et al. 2013)	50 Subplots totaling 400 measures
Respiration	Spatial	Amount of CO_2 released. Measured in μmol CO_2 m^{-2} s^{-1}. More released CO_2 is related to higher soil respiration, which in turn is associated with greater (i) microbial activity, (ii) release of nutrients contained in organic matter, (ii) and resources for ants (Kaspari et al. 2010)	50 Subplots totaling 300 measures
Trees	Spatial	Richness of tree species over 10 cm in diameter at breast height per plot. Measured in number of species. Reducing tree richness simplifies food and nesting resources for ants (Klimes et al. 2012)	50 Subplots totaling 266 recorded tree species
DBH	Spatial	Mean diameter at breast height (DBH), per plot, of individuals over 10 cm in diameter. Measured in centimeters. Reducing DBH leads to reduction in biomass production and affects litter conditions for ants (Klimes et al. 2012; Bujan et al. 2016)	50 Subplots totaling 1040 recorded individuals

The response variable in each model was species richness or species composition. The temporal data were defined as the 8 months of sampling in each site ($N=16$). The spatial data were defined as the twenty-five 20 × 20 m subplots in each site ($N=50$). Additional information on data collection can be found in the Supporting Information

of importance and analyzed in a stratified manner (“strata” argument), considering the paired sampling design. Redundancy analysis (RDA) was used to visualize ordinations using the “rda” function in the package *vegan* (Oksanen et al. 2020); the Bray–Curtis index was used as the distance measure in the ordinations (Gotelli and Ellison 2012).

Finally, based on ant data collected in 2011–2012, we classified species as specialists in the control and induced drought plots using a Multinomial Species Classification Method (CLAM) as implemented in the “clamtest” function of the *vegan* package (Oksanen et al. 2020). This test places species in four groups based on their frequency of occurrence, allowing for a robust statistical classification with no need to exclude rare species (Chazdon et al. 2011). The four species groups tested were: (i) preferentially occurring in the control plot; (ii) preferentially occurring in the induced drought plot; (iii) no preference between categories or generalists; and (iv) species with a low sampling number or uncommon in the study area, unable to confidently attribute any of the three previous classifications. We used a predefined specialization value = 66%.

The figures were plotted using *ggplot2* (Wickham 2016), *GGally* (Schloerke et al. 2021) and *cowplot* (Wilke 2020).

Results

In total, we collected 217 ground-dwelling ant species, belonging to 54 genera and 8 subfamilies across the 2 ESECAFLOR plots (Supporting Information, Table S1). We recorded 172 ant species in the control plot and 157 species in the induced drought plot; 112 species were recorded in both plots. The richest genus was *Pheidole* (43 species), followed by *Neivamyrmex*, *Gnamptogenys*, and *Strumigenys* (10 species each).

The model that best explained temporal changes in ant species richness included experimental treatment (plot), litter diversity, and their interaction (Fig. 2a and b; Supporting Information, Table S2). Fourteen spatial models had ΔAICc values < 2 (Supporting Information, Table S2), and variously included experimental treatment, litter diversity, and tree species richness (Fig. 2d and e). All other variables

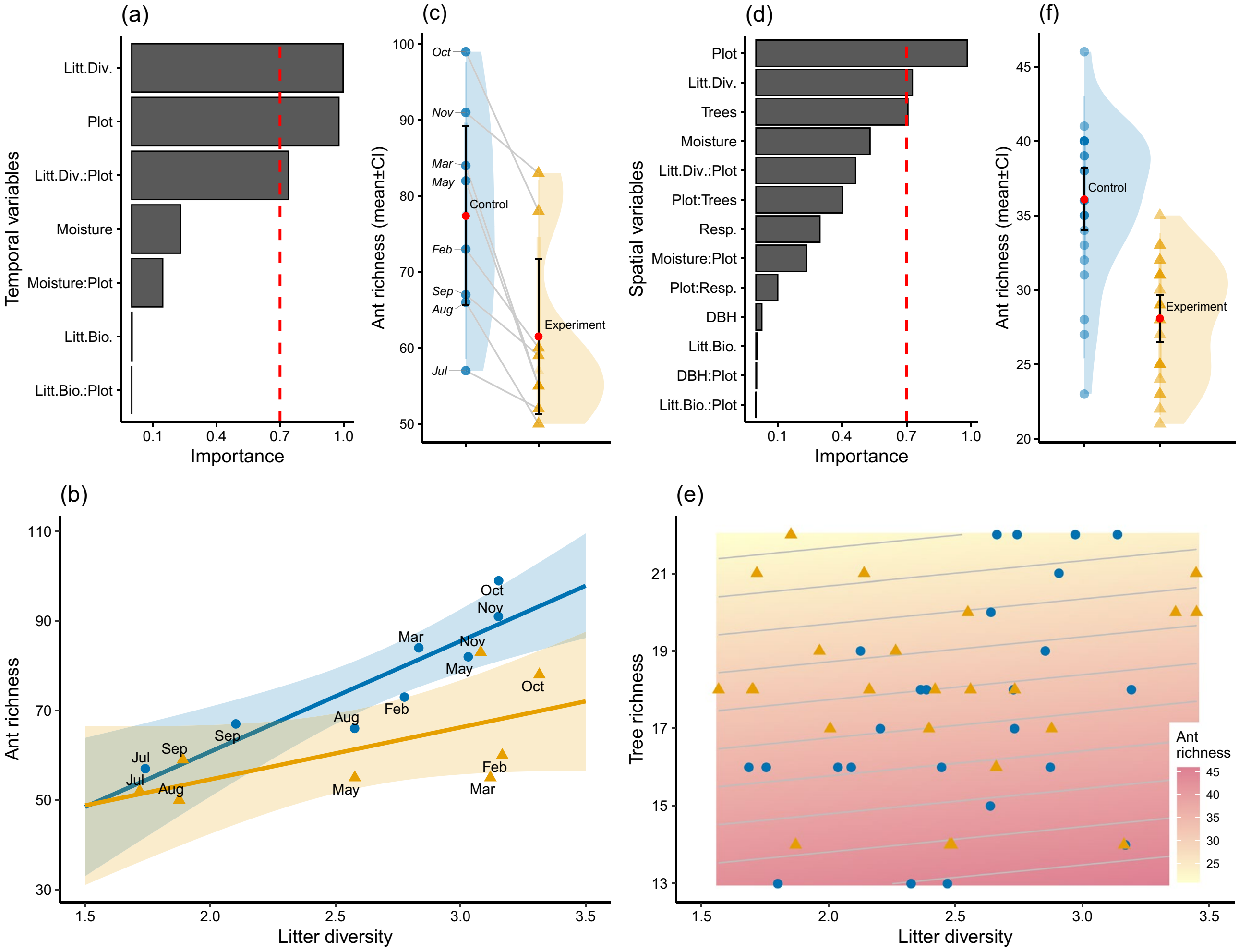

Fig. 2 The relative importance of each variable in the best fitting **a** temporal model (litter diversity 0.99, plot 0.98, and the interaction between litter diversity and plot 0.74) and **d** spatial model (plot 0.98, litter diversity 0.73, and tree richness 0.71) on ant species richness. The vertical red lines represent cuts in variable importance (at importance = 0.7). *Litt.Div.* Litter diversity, *Litt.Bio.* Litter biomass, *Resp.* Respiration, *DBH* Diameter at breast height. Relationship between **b** litter diversity and ant richness in the temporal model and **e** litter diversity and tree richness and the ant richness in the spatial model. Ants were collected in **c** months and **f** subplots in the control and experimental plot of ESECAFLOR, Pará, Brazil. Blue circles: control plot; yellow triangles: experimental plot; red circles: mean richness. See Supporting Information (Table S2) for additional information of best models

in both models had ΔAICc values < 0.7 (Fig. 2a and d). The experimental plot had significantly lower species richness for both the temporal (control = 77 ± 11.8; induced drought = 62 ± 10.2; $t_7 = 4.96$, $p = 0.001$; Fig. 2c) and the spatial model (control = 36 ± 2.1; induced drought = 28 ± 1.6; $t_{44.93} = 6.26$, $p < 0.001$; Fig. 2f).

Ant species composition differed in the control and induced-drought plots (Table 2)–the experimental treatment was characterized by an increased frequency of generalist species. Further, species composition was negatively influenced by soil moisture (spatial and temporal models), and litter diversity (temporal model only) (Fig. 3; Table 2). For the temporal model, RDA explained 29.3% of the total variation on the first two axes (Supporting Information, Table S3). Moisture had the strongest contribution to axis 1 and was associated with the species group in the control plot. Litter diversity had the strongest contribution to axis 2 (Fig. 3a). For the spatial model, the first two axes of the RDA explained < 10% of the total variation in the data. Soil moisture again loaded most strongly on axis 1 (Fig. 3b; Supporting Information, Table S3).

Finally, we found specialist species in both the experimental and control plots (Fig. 4). Multinomial classification identified 12 specialists in the control plot (*Neoponera verenae*, *Ochetomyrmex neopolitus*, *Oc. semipolitus*, *Odontomachus* nr. *bauri*, *Od.* nr. *haematodus*, *Octostruma betschi*, *Pheidole cursor*, *P. jeannei*, *Pheidole* in the *Fallax* group, and *Pheidole* sp., *Strumigenys denticulata* and *Solenopsis* nr. *virulens*) and 12 species in induced-drought plot (*Apterostigma* nr. *pilosum*, *Mayaponera constricta*, *M. arhuaca*,

Table 2 PERMANOVA analysis describing the relationship between ant composition and environmental variables for the temporal (moisture, litter diversity, and litter biomass) and spatial (moisture, litter diversity, litter biomass, respiration, trees, and DBH) models

Model	Predictor	*df*	SS	MS	*Pseudo* F	R^2	*p*
Temporal	Soil moisture	1	0.35	0.35	4.85	0.21	**< 0.001**
	Litter diversity	1	0.28	0.28	3.80	0.16	**< 0.001**
	Plot	1	0.21	0.21	2.86	0.12	**0.002**
	Litter biomass	1	0.07	0.07	0.99	0.04	0.42
	Residual	11	0.80	0.07		0.47	
	Total	15	1.71			1	
Spatial	Soil moisture	1	0.80	0.80	3.91	0.07	**< 0.001**
	Litter diversity	1	0.16	0.16	0.80	0.02	0.78
	Plot	1	0.38	0.38	1.86	0.04	**< 0.01**
	Litter biomass	1	0.18	0.18	0.88	0.02	0.65
	Respiration	1	0.31	0.31	1.50	0.03	0.05
	Trees	1	0.16	0.16	0.78	0.01	0.78
	DBH	1	0.25	0.25	1.22	0.02	0.18
	Residual	42	8.61	0.21		0.79	
	Total	49	10.8			1	

Significant p values ($p < 0.05$) are in bold

SS Sum of squares; *MS* Mean of squares; p values determined by permutation

Neivamyrmex pseudops, *Pachycondyla crassinoda*, *Paratrachymyrmex* nr. *bugnioni*, *Pheidole bruesi*, *P. triconstricta*, and an unnamed species of each of *Azteca*, *Crematogaster*, *Neivamyrmex*, and *Nylanderia).* Of the remaining species, 44 (20%) showed no preference among plots and 149 (69%) occurred at such low frequencies that plot preferences could not be determined (Fig. 4).

Discussion

We hypothesized that in the ESECAFLOR plots that ant species richness should be lower in the experimental (induced-drought) plot and that relative abundance of different ant species should change when drought was induced. Based on 1 year of sampling, we found both reduced species richness and relative abundance of ants in a primary Amazonian rainforest subject to experimentally induced drought. These changes in the structure of ant assemblages were associated with reductions in soil moisture content and litter diversity that occurred following the induced drought. We also identified some ant species that increased in abundance or occurred uniquely in the induced-drought conditions. We note that our study design is limited by a combined lack of replication and pre-treatment data. Given those limitations, our results suggest rather than conclusively demonstrate impacts of drought on ant assemblages.

Species richness

In tropical forests, ants have different strategies to avoid desiccation, such as foraging at night or within plant litter (Kaspari and Weiser 2000). However, the combination of high temperatures and reduced precipitation may reduce the survival or competitive ability of some tropical forest species (Debinski et al. 2013; Diamond et al. 2016). In parallel with other studies in tropical wet forests (e.g., Vasconcelos et al. 2010; Baccaro et al. 2013), we also found that ant species richness was lower when rainfall was excluded.

Habitat complexity is an important parameter for understanding the capacity of a habitat to harbor higher ant richness during droughts. Plant litter quality is often a predictor of arthropod richness, and litter quality in turn is connected to a higher soil moisture capacity, which enables ground-dwelling animals to better cope with drought conditions (Richardson et al. 2005). Heterogeneity or the diversity of items comprising plant litter can be a predictor of ant diversity in tropical forests (Queiroz et al. 2013). For example, extended periods of drought can reduce coarse woody debris (Rowland et al. 2018), which in turn reduces the abundance and diversity of twig-nesting ants (Fernandes et al. 2019). Although there is a well-known, positive relationship between litter diversity and ant richness (Armbrecht and Perfecto 1979; Almeida et al. 2021), increasing dryness in our experiment made this effect less pronounced (Fig. 2b).

Species composition

Species composition differed between the 1-ha control plot and the 1-ha induced-drought plot. Compositional changes as a function of drought induced by climatic change have been reported previously for butterflies (Carnicer et al. 2019), birds, and fishes (Costa et al. 2020). The loss of soil moisture resulting from reduction in precipitation,

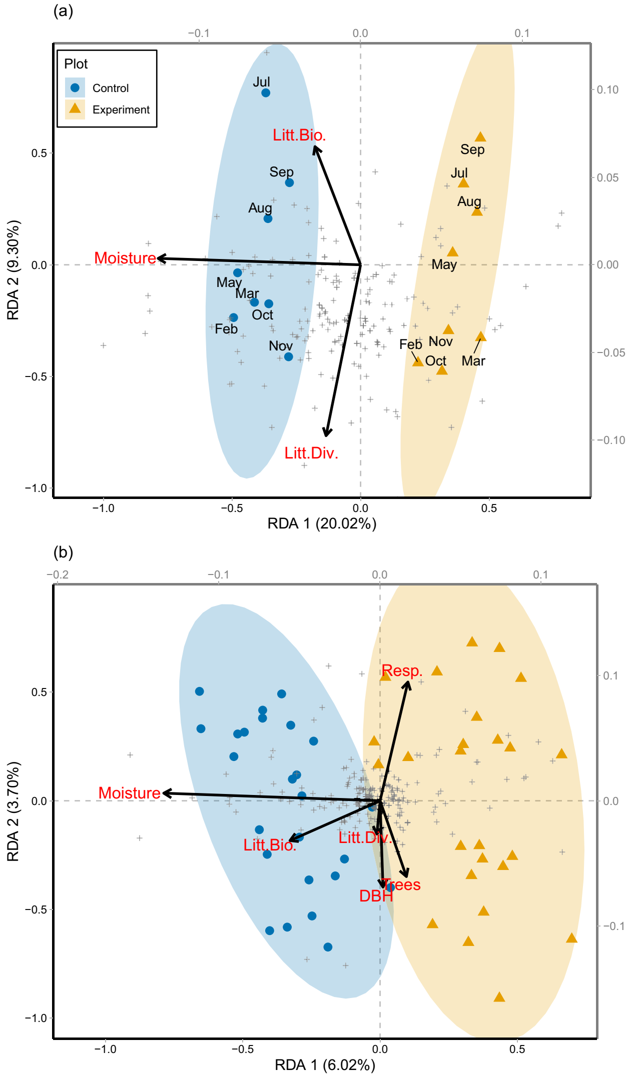

Fig. 3 RDA results for the **A** temporal and **B** spatial models of ant assemblages in the control (blue) and experimental (yellow) plots (statistics in Table 2). Abbreviated variable names as in Fig. 2. Eigenvalues and variance explained for the main components were described in Supporting Information Table S3. Grey points represent the locations in ordination space of the 217 ant species collected

seasonal flooding, or deeper groundwater also can directly affect ant assemblages (Vasconcelos et al. 2010; Baccaro et al. 2013). In periods of drought in tropical forests, some ant guilds (e.g., raid-hunting predators) are rare or absent, but others (e.g., cryptobiotic fungus-farmers) are unaffected or increase in abundance (Costa et al. 2020). The reduction of water availability in tropical forests also can affect ants indirectly through its effects on trees. For example, a lower diversity of items in the litter can affect the taxonomic and functional diversity of ant communities (Folgarait 1998; Coyle et al. 2017), with long-term effects on environmental recovery (Martello et al. 2018).

Our study also suggested a relationship between changes in ant composition and water availability (Vasconcelos et al. 2010; Baccaro et al. 2013), and between ant composition and environmental heterogeneity (Delsinne et al. 2013; Guilherme et al. 2021). Our data also showed that temporal effects are stronger and more easily detected than spatial effects, a result that could be related to the reduced grain-size in the spatial analyses (i.e., larger replicated plots would be better to use to identify environmental filters of community structure (Delsinne et al. 2013).

Species associations

Our data clearly identify thermophilic and generalist species associated with simplified environments when drought was induced in an otherwise wet tropical forest. For example, fungus-growing ants (*Apterostigma* and *Paratrachymyrmex* spp.) were associated with the drier (experimental) conditions. These genera also have also been found to increase in frequency in fragmented or simplified environments (Ribas et al. 2012; Baccaro et al. 2013), where their drought tolerance was related to their nesting under trunks or in the ground rather than directly on the leaf-litter. Other taxa that thrived under induced-drought conditions were members of generalist taxa (*Azteca, Crematogaster, Nylanderia, Pheidole*; Ribas et al. 2012; Silva and Brandão 2014). In contrast, large-sized species showed idiosyncratic responses to drought tolerance: three large epigeic predators were more common in the induced drought plot (*Mayaponera constricta*, *M. arhuaca* and *Pachycondyla crassinoda*) and three were more common in the control plot (*Odontomachus* nr. *haematodus*, *O.* nr. *bauri* and *Neoponera verenae*).

In summary, induced drought appeared to affect ant assemblages, reducing their richness and altering their species composition, mainly through the increased occurrence and abundance of thermophilic and generalist species. When throughfall was experimentally reduced in an Amazonian forest, consequent effects of induced drought—variability in biomass and soil moisture—were the most important predictors of species richness and composition of ground-dwelling ant species. Our study suggests adverse effects could be caused by prolonged droughts on ant assemblages in Amazonian forests. In turn, these shifts would be expected to cascade onto ecosystem processes and services provided by ants.

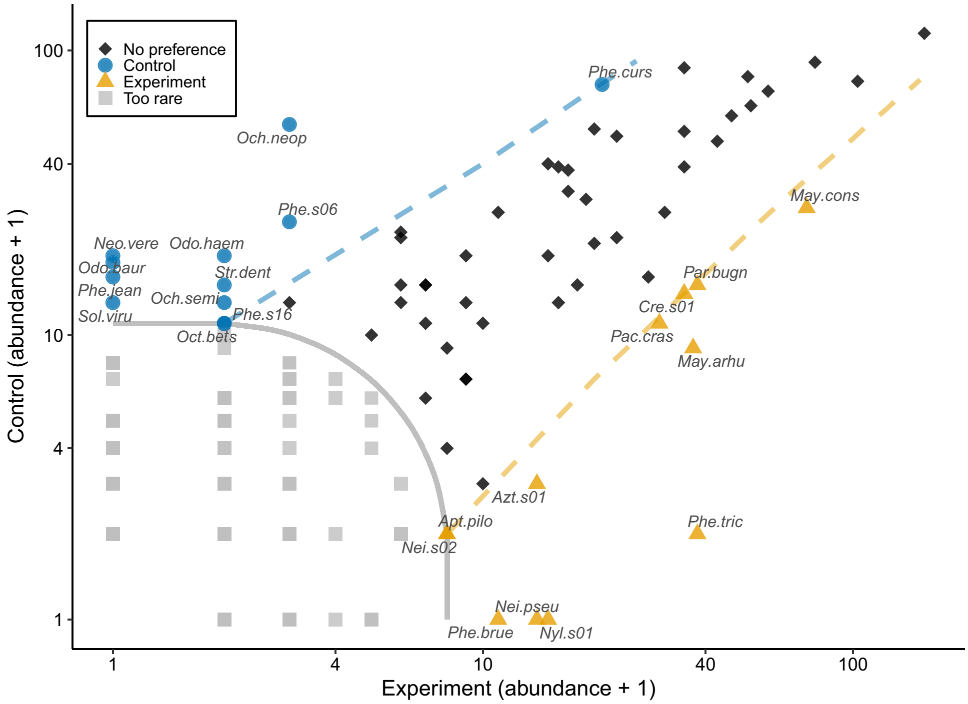

Fig. 4 CLAM analysis classifying the 217 collected ant species into four classes based on their frequency of occurrence in the control and experimental plots: no preference or generalists (black diamonds); too rare to be assigned a preference (gray squares); associated with the control plot (i.e., natural forest) (blue circles): associated with the experimental plot (i.e., drought-induced forest) (yellow triangles). Species codes given in Supporting Information, Table S1

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-023-05316-x.

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Author contribution statement ACLC, LVF, and PM conceived of the idea and designed the research; ACLC and LVF carried out the fieldwork; RPSA performed the material processing; RPSA analyzed the data with significant input from RRS; RPSA led the writing of the manuscript with significant help from RRS and AME; All authors contributed critically to the drafts and gave final approval for publication.

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Data availability All data and R code are available from the Harvard Forest Data Archive and the Environmental Data Initiative, https://doi.org/10.6073/pasta/19da2e541f37c859e3ea702436cf6b50 (Almeida 2020).

Declarations

Conflict of interest The authors have not disclosed any competing interests.

Ethical approval Ethics approval was not required for this study according to local legislation.

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