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Arboreal ant abundance tracks primary productivity in an Amazonian whitewater river system

Elizabeth G. Pringle [1],†, Talitha Ferreira dos Santos [2], Marcelle S. Gonçalves,[2]
Joseph E. Hawes,[3] Carlos A. Peres,[4,5] and Fabricio B. Baccaro[2]

[1]Department of Biology, Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, Reno, Nevada, USA
[2]Departamento de Biologia, Universidade Federal do Amazonas, Manaus, Brazil
[3]Applied Ecology Research Group, School of Life Sciences, Anglia Ruskin University, Cambridge, UK
[4]School of Environmental Sciences, University of East Anglia, Norwich, UK
[5]Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, Brazil

Abstract. Little is known about consumer productivity in the tropics despite the key feedbacks that animals impose on primary productivity. In the Amazon basin, seasonally flooded and unflooded forests exist side by side, and ants (Formicidae) dominate animal biomass. Although flooding has a direct negative effect on soil-dwelling ants, it is less clear whether flooding has indirect effects on arboreal ants via associated changes in tree communities. To test whether seasonal inundation by whitewater affects arboreal ants, we investigated ant communities in adjacent flooded and unflooded forests along a major whitewater river in central-western Amazonia. Whitewater-flooded forest exhibits higher primary productivity than unflooded forest. We thus hypothesized that forest type would affect the productivity and the foraging traits of arboreal ants and that these changes would be mediated by increases in plant-derived food for ants in flooded forest. We compared ant and plant communities between flooded- and unflooded-forest transects along the Juruá River in Amazonas, Brazil. We collected, identified, and counted terrestrial and arboreal ants, and we measured ant traits with putative relationships to foraging strategy. We also identified plant stems to characterize the abundance of ant food rewards. Flooding negatively affected the diversity and abundance of terrestrial ants but did not change the diversity of arboreal ants. Arboreal ants were more abundant and exhibited higher biomass in flooded forest than in unflooded forest. Arboreal ant traits also suggested that ants may rely more heavily on plant-derived food in flooded forest than in unflooded forest. These differences were associated with a higher abundance of plant stems predicted to contain ant food rewards in flooded forest than in unflooded forest. Our results indicate that the productivity of arboreal ants is affected by that of the underlying forest. Such effects may be mediated by the predominantly herbivorous foraging strategy of canopy ants, which would link ant populations closely to primary production and stoichiometry. Given ants' important functional roles, these differences in ant productivity between forest types may have consequences for other arthropods and feedbacks to plants throughout the Amazon basin.

† **E-mail:** epringle@unr.edu

INTRODUCTION

Given the importance of tropical forests to Earth's net primary productivity (NPP) and the potential for animals to impose important feedbacks on primary production (e.g., Asner et al. 2010, Terborgh 2012, Sobral et al. 2017), we know surprisingly little about variation in consumer abundance or biomass in tropical forests (McNaughton et al. 1989). A logical prediction is that higher primary productivity should increase animal productivity, as has been seen in other systems such as temperate grasslands (Borer et al. 2012) and tropical savannas (Pringle et al. 2010). Yet despite clear relationships between plant and animal diversity in tropical forests (Basset et al. 2012), links between plant and animal productivity have not yet been clearly established (Whitfeld et al. 2012, Schuldt et al. 2014). To the extent that these links exist, they may decrease in strength as animals move up the trophic chain (Scherber et al. 2010), such that plant productivity is linked more strongly to herbivores than to predators and predator-driven trophic cascades.

The Amazon basin comprises a mixture of upland and wetland forests along whitewater, blackwater, and clearwater rivers, and these forests vary markedly in their respective productivities (Junk et al. 2011). Whitewater rivers are unique because they carry nutrient-rich sediments derived from their Andean headwaters, which they deposit onto downstream floodplains during annual flood pulses. These whitewater-flooded forests, known as *várzea*, cover more than 400,000 km^2 or ~6% of the Amazon basin (Melack and Hess 2010). Várzea forest exists alongside upland, or *terra firme*, unflooded forest that grows above the flood pulse. Although direct comparisons of tree communities between adjacent várzea and terra firme forests are limited, várzea forest soils can contain 20 × more phosphorus and 360 × more potassium than terra firme forest soils (Worbes 1997). Thus, despite the disturbance caused by floods and the accompanying stress of prolonged root submersion (Parolin 2001), which decrease tree standing biomass and the floral and faunal diversity of várzea relative to terra firme (e.g., Campbell et al. 1986, Majer and Delabie 1994, Peres 1997*b*, Haugaasen and Peres 2005, Hawes et al. 2012), várzea forest trees produce higher relative fruit biomass and lower wood densities than terra firme forest trees (Hawes et al. 2012, Hawes and Peres 2016). Wood density is negatively correlated with growth rates in the Amazon (Chao et al. 2008), and both fruit production and wood density thus indicate higher rates of aboveground carbon fixation in várzea than in terra firme.

Ants (Hymenoptera: Formicidae) attain extremely high diversity and biomass—possibly even dominating overall animal biomass—in the Amazon (Fittkau and Klinge 1973, Hölldobler and Wilson 1990). Amazonian ants are diverse and abundant in both terrestrial and arboreal habitats, with distinctive generic communities in each stratum (Wilson 1987). Soil- and litter-nesting ant communities are strongly affected by forest type: Floodwaters have a direct negative impact on ground-nesting ants (Mertl et al. 2009, Vasconcelos et al. 2010), which reduces their diversity and abundance in flooded forest (Majer and Delabie 1994, Vasconcelos et al. 2010). It is less clear whether and how flooding also affects arboreal ants, which are above the reach of floodwaters. Most flooded-forest ant species are arboreal nesters (Majer and Delabie 1994), and vertical migration of predominantly terrestrial taxa during inundations has been observed (Adis 1982). The scant comparisons of arboreal insect communities between flooded and unflooded Amazonian forests are based on canopy fogging of single transects and give conflicting evidence: Among várzea, terra firme, and blackwater-flooded forests, várzea is reported to have either the highest (Erwin 1983) or the lowest (Adis et al. 1984) abundance of arboreal ants. These two studies were conducted one year apart, in the same season, and at nearby várzea and terra firme locations, but Adis et al. (1984) suggested that differences in tree communities between the two studies might explain their conflicting results.

The composition, stoichiometry, and ecophysiology of tree communities should indeed be the nexus between the differential resources of flooded and unflooded forest and differences in arboreal ant communities. Studies of Amazonian vertebrate communities have found that nonvolant arboreal mammals, including primates, exhibit twice the estimated total biomass in várzea than in adjacent terra firme forest (Peres 1997*b*, Haugaasen and Peres 2005). These differences exist despite the lower species richness of both

primates and other mammals in várzea. The nutrient-rich soils of flooded forest should increase the nutrient:carbon ratio of foliage, which has been shown to increase the biomass of folivorous primates (Ganzhorn 1992, Peres 1997a). Floods also increase the structural heterogeneity of flooded forest, reduce leaf longevity, and increase leaf turnover (Campbell et al. 1986, Parolin et al. 2010, Wittmann et al. 2010), all of which should favor the production of more new foliage with higher nutritional value for consumers (Coley 1983).

Ants are not folivores, but the enormous biomass of ants in tropical forests is suggested to result partly from the foraging of many dominant canopy ant species as cryptic herbivores that feed on the exudates of plants and phloem-feeding hemipterans (Davidson et al. 2003). Arboreal ants may thus be strongly affected by bottom-up trophic cascades, mediated by differences in primary productivity and associated chemistry. Increases in ant productivity would also have the potential to produce stronger top-down effects in more productive arboreal systems due to the ornery behaviors of dominant canopy ant species, even if they are not true predators (Davidson 1998). To identify herbivory as a mechanism linking primary productivity to ant productivity, it would be useful to identify morphological traits that indicate shifts in diet and foraging habits among arboreal ants along the omnivorous continuum between herbivory and predation. The foraging functional types of litter-nesting ant species have been studied to some extent (e.g., Delabie et al. 2005, Weiser and Kaspari 2006, Silva and Brandão 2010, Gibb et al. 2015), and these studies suggest the importance to predators of traits such as large mandibles, short eye-to-mandible distances, and large petioles. Comparatively little is known about the traits that identify tree-nesting cryptic herbivores, although longer heads and longer clypei may contribute to effective liquid feeding and smaller body size may be associated with hemipteran tending (Davidson et al. 2004, Parr et al. 2017). The functional relevance of these morphological traits can be tested by examining their relationships to nitrogen isotopes, which get heavier up the trophic chain.

Here, we sought to test the hypothesis that the differences in primary productivity between adjacent whitewater-flooded and unflooded forests would affect the productivity and the foraging traits of arboreal ant communities in the Amazon. To do this, we conducted a study of arboreal ant communities along the Juruá River in central-western Amazonia. We included terrestrial ants for comparison and to rule out vertical compression of terrestrial ants in flooded forest as a cause of arboreal patterns. We predicted that higher primary productivity in flooded forest would increase arboreal ant abundance and biomass, but that these effects might not be associated with effects on diversity. We further predicted that these effects would be mediated by shifts in arboreal ant foraging strategy, wherein a more herbivorous strategy would be more prevalent among flooded-forest arboreal ants and would be supported by a higher supply of plant-associated food rewards in these highly productive forests.

METHODS

Study area

The study was conducted along the Juruá River within two contiguous forest reserves—the Médio Juruá Extractive Reserve (253,227 ha) and the Uacari Sustainable Development Reserve (632,949 ha)—in the state of Amazonas, Brazil. The Juruá River is a major whitewater tributary of the Amazon River that carries particularly dense sediment loads (Assis et al. 2015) and supports a wide swath (20–45 km) of high-fertility várzea floodplain. The region has a wet tropical climate: At the Bauana Field Station (5°26′S, 67°17′W), located within 10 km of 8 of our 14 transects, the mean annual temperature is 27.1°C and rainfall averaged 3679 mm/yr between 2008 and 2010. The river rises up to ~14 m each rainy season, bringing ~2–5 m of standing water into the flooded forest from ~January to June each year (Hawes and Peres 2016). The region conforms to the typically low levels of floristic similarity between flooded and unflooded forests (approximately 10–30%; Wittmann et al. 2010), but the stem density of trees ≥10 cm in diameter at breast height is statistically indistinguishable between flooded and unflooded forests (Hawes et al. 2012).

Ant sampling

To compare ant communities between the two forest types, we selected seven pairs of flooded- and unflooded-forest transects for sampling ($N = 14$),

with each pair located at a similar latitude and longitude along ~170 km of the meandering river (~80 km in a straight line; average distance between paired transects = 5.9 km; Appendix S1: Fig. S1). We maximized sampling on both sides of the river and, when possible, kept both paired transects on the same side of the river (4/7 pairs). Each 100-m transect was located haphazardly within the selected areas but avoiding trails and canopy gaps. We sampled terrestrial ants in each transect using (1) 10 cm diameter pitfall traps, spaced at 10-m intervals ($n = 10$), and (2) a Winkler sack filled with 18 L of litter collected over the entire transect at similar intervals ($n = 1$). We sampled arboreal ants every 15 m in each transect by (1) beating understory plants ($\sim \leq 3$ m tall) for 2 min onto a 1-m^2 beat sheet and collecting all ants that fell onto the sheet ($n = 5$), and (2) hanging 10 cm diameter pitfall traps ~20 m high in the canopy ($n = 5$). Arboreal pitfall traps were baited with sardine oil and hung using a pulley system after hooking the desired branch with a slingshot and a weight tied to a spool of fishing line (Video S1). Arboreal pitfall traps were adjusted so that they were touching at least one tree branch. Both terrestrial and arboreal pitfall traps contained 93% ethanol with a drop of detergent and were left in the field for 48 h. Winkler sacks were hung at camp for 48 h at ambient temperature. We sampled terrestrial and arboreal ants in all transects in the dry season of September 2014, and we sampled terrestrial ants in unflooded-forest transects and arboreal ants in all transects in the rainy season of April–May 2015. We used the same locations for ground and arboreal pitfalls in both seasons.

To process these collections, the ants from all individual traps (i.e., individual samples from each of the four sampling methods described above) were identified to species whenever possible (61%) and otherwise to morphospecies. We used two measures of the abundance of morphospecies: "Occurrence" was quantified as the presence/absence of each morphospecies per trap, and "abundance" was quantified by counting all individuals of each morphospecies per trap (Gibb et al. 2017). Because ants are social insects, occurrence data approximate the number of ant colonies per locality and were used to assess diversity, whereas abundance data were used to assess colony productivity (Gotelli et al. 2011). To

investigate potential mechanisms driving differences in ant communities between forest types, up to six individuals of each morphospecies were used to measure the following traits with putative relationships to foraging strategies (see, e.g., Parr et al. 2017): mesosomal length (i.e., Weber's length), head length, clypeus length, petiole size (height × width), mandible length, and distance from eyes to mandibular insertion. Measurements of pinned specimens were made using Leica Application Suite, version 4.8.0, attached to a Leica M 125 stereomicroscope. We used the highest magnification that allowed the measured trait to fit within the ocular range.

Nitrogen isotopes can provide insight into ant trophic position at macroecological scales (Fiedler et al. 2007). It was not possible to analyze stable isotopes in our collections from the Juruá study landscape, so we estimated the relative trophic position of our ant genera using ant collections at the Field Museum (Chicago, Illinois, USA) from Australia, Costa Rica, Florida, and Uganda, preserved in 95% ethanol at $-20°C$ until time of dissection (C. S. Moreau, *unpublished data*). To obtain enough sample material, 3–20 individual ants, excluding abdomens (Smith and Tillberg 2009), were included in each sample. Samples were dried in an oven at 50°C and weighed into tin capsules using a microbalance. All analyses were performed at the Stable Isotope Ratio Facility for Environmental Research at the University of Utah. Additional isotope data were included from Davidson et al. (2003) and Tillberg et al. (2007). We calculated the average trophic position for each ant genus by combining samples from multiple species or samples, when possible (average N per genus = 9). We corrected for between-site differences in nitrogen isotope ratios by subtracting each site's average plant $\delta^{15}N$ from the respective, sympatric ant $\delta^{15}N$ ($\delta^{15}N_{ant} - \delta^{15}N_{plant}$; Feldhaar et al. 2010).

Plant communities

To investigate the possibility that plant-derived resources for arboreal ants are different between forest types, we examined the potential abundance of extrafloral nectar and myrmecophytic hemipterans in plant communities. All live stems ≥ 10 cm in diameter at breast height were surveyed between 2008 and 2011 in 26 0.1-ha tree

plots (100 × 10 m) in six transects (n = 3 transects in unflooded forest, three transects in flooded forest) adjacent to the transects where we surveyed ants (Appendix S1: Fig. S1; Hawes et al. 2012). Stems were identified to the lowest possible taxonomic level by a local field assistant, and identities were verified by a technician from the Botany Department of the Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus). Of the 1595 stems surveyed, 23.6% of stems were identified to species and another 54.3% of stems were identified to genus. Recorded stems included palms but excluded woody lianas and hemi-epiphytes. For more details, see Hawes et al. (2012).

Using a world list of plants with extrafloral nectaries (Weber et al. 2015) and a list of myrmecophytic plants that specifies ant food rewards (Davidson and McKey 1993), including both extrafloral nectar and myrmecophytic hemipterans, we assigned each stem with a verified species or genus name to a binary category indicating whether that taxon is reported to have extrafloral nectaries or myrmecophytic hemipterans (1) or not (0). We assigned probable nectar presence/absence to 75% (519/693) of the stems in unflooded forest and to 80% (728/902) of the stems in flooded forest. Although there can be variation within genera in the presence of extrafloral nectaries, we assumed that this error would be distributed unbiasedly between stems in unflooded and flooded forests.

Analysis and statistics

All analyses and statistics were conducted in R v3.4.3 (R Core Team 2017).

Ant diversity.—To compare ant diversity among factorial combinations of forest type and stratum, we conducted analyses of alpha and beta diversity using the vegan package (Okansen et al. 2017). To investigate alpha diversity, we estimated species richness using species accumulation curves (*specaccum* function, method = exact) based on all traps per forest type (unflooded or flooded) and stratum (terrestrial or arboreal). We also calculated inverse Simpson indices using transects as replicates (n = 7 per forest type) and species occurrences as abundance data. We tested for differences among diversity indices using two-way ANOVA with post hoc Tukey's HSD.

To investigate the beta diversity of ant communities between unflooded and flood forest and between terrestrial and arboreal strata, we conducted nonmetric multidimensional scaling analyses of occurrences (i.e., ant colony abundance) per transect using Bray-Curtis dissimilarities for both genera and morphospecies. We tested for differences in ant community structure among strata and forest types using permutational multivariate analysis of variance (PERMANOVA, *adonis* function in the vegan package).

Ant abundance and biomass.—To investigate patterns in ant abundance, we compared species occurrences and abundances between forest types. Abundance data were analyzed using generalized linear mixed models (GLMMs) with a Poisson or negative binomial distribution and traps as replicates using the glmmTMB package in R (Brooks et al. 2017). Because sampling of terrestrial ants in flooded forest was necessarily restricted to the dry season, we used only dry-season data to compare terrestrial ants between forest types and conducted a separate analysis for arboreal ants in both seasons. To account for non-independence of multiple traps from the same transect, we compared transect nested within block—a variable indicating the river section (Appendix S1: Fig. S1)—or transect alone as random intercept effects and used the model with the lowest Akaike information criterion (AIC). We used forest type, trapping method, and season (the latter for the arboreal stratum only) as potential fixed effects. We also compared terrestrial ant abundances between the dry and high-water seasons in unflooded forest. We used backward selection, beginning with the most complex model and stepping down. We compared nested models by AIC and chi-square tests. To calculate test statistics for the conditional fixed effects, we used type II Wald chi-square tests in the car package in R (Fox and Weisberg 2011). To calculate effect sizes, we used the effects package in R (Fox 2003, Fox and Weisberg 2018). In cases where the best model included an interaction effect between factors, we summarized effect sizes for each factor by averaging across all levels of the other factors. Ant abundances produced highly right-skewed distributions; for these data, we thus also compared GLMMs with raw data to linear mixed models (LMMs) using Box-Cox transformed data.

Once forest type was selected as a factor explaining arboreal ant abundances, we conducted additional analyses of the abundance

distributions, which exhibited unusually long tails. We compared different distribution fits to log-transformed data in the fitdistrplus package in R using AIC and visual examinations of predicted and empirical probabilities (Delignette-Muller and Dutang 2015). The Weibull distribution, a generalization of the exponential distribution that employs both a shape and a scale parameter (where the shape parameter in an exponential distribution always equals one, and scale indicates the extent of the distribution) (Cullen and Frey 1999), provided the best fit to the right tail of the data (Appendix S1: Table S1 and Fig. S2). We summarized the differences in the Weibull distributions of abundance data between forest types using 1000 bootstrap replicates to estimate both the shape and scale parameters, as well as the 75% quantile of each distribution.

To test whether differences in arboreal ant abundance translated into differences in ant biomass between unflooded and flooded forest, we estimated ant biomass per trap by multiplying average ant mesosomal length (a proxy for ant body size) per trap by the corresponding number of ants in that trap (Kaspari and Weiser 1999). To investigate whether ant biomass was different between forest types, we used GLMM comparisons as described above for ant abundance.

Ant traits.—To investigate potential variation in foraging strategies between forest types, we analyzed differences in the morphological traits of arboreal ants between unflooded and flooded forests. We used mesosomal length as a proxy for ant body size. We standardized each of the other five traits (head length, clypeus length, petiole size, mandible length, and eye-to-mandible distance) by body size by dividing the mean trait value for each morphospecies by its mean mesosomal length. We calculated principal components for these five traits at the morphospecies level (*prcomp* function with unit scaling; R Core Team 2017). We then calculated means per trap of trait values by morphospecies occurrences for analysis of LMMs and multivariate analysis of variance (MANOVA).

To determine whether body size and trait syndromes of arboreal ants were different between forest types, we used backward selection in LMMs in the lme4 package in R (Bates et al. 2015), with river section and transect as alternative random intercept effects and forest type, season, collection method, and their interactions as potential fixed effects. To test whether disparity in trait syndromes differed between flooded and unflooded forests, we conducted MANOVA on the five principal components by forest type, in this case pooling averages per trap across collection methods (beating and arboreal pitfall) and seasons (high-water and low-water).

Finally, to investigate the potential functional relationship between morphological traits and ant foraging strategy, we analyzed regression relationships between our traits, averaged within genera, and the respective mean generic nitrogen isotopes (δ^{15}N) values, which are positively related to trophic level (Davidson et al. 2003). We conducted both non-phylogenetic and phylogenetically corrected regressions. Regressions were conducted using the *lm* function in R (R Core Team 2017). Phylogenetically independent contrasts were calculated in the ape package in R (Paradis and Schliep 2018) using a tree adapted from several recent phylogenies (Moreau and Bell 2013, Schmidt 2013, Ward et al. 2016, Branstetter et al. 2017, Appendix S2). We also conducted tests of trait phylogenetic signal using Blomberg's *K* statistic (Blomberg et al. 2003) in the phytools package in R (Revell 2012).

Plant communities.—To test for differences in the abundance of stems with extrafloral nectaries and myrmecophytic hemipterans between forest types, we used GLMMs with a binomial distribution in the package glmmTMB in R (Brooks et al. 2017). Tree plot was used as a random effect, and forest type was used as a potential fixed effect. Test statistics were determined in the car package using Type II Wald chi-square tests (Fox and Weisberg 2011). Effect sizes were determined in the effects package (Fox 2003, Fox and Weisberg 2018).

RESULTS

Ant diversity

We collected and identified 17,693 ants, representing 1,594 unique occurrences of 211 morphospecies belonging to 47 genera in eight subfamilies (from highest to lowest number of occurrences: Myrmicinae, Formicinae, Ponerinae, Dolichoderinae, Ectatomminae, Pseudomyrmecinae, Dorylinae, and Amblyoponinae; Appendix S3).

Terrestrial ants in unflooded forest exhibited the highest morphospecies richness among all

combinations of stratum and forest type (unflooded forest, terrestrial = 52 ± 3, arboreal = 24 ± 1; flooded forest, terrestrial = 16 ± 2, arboreal, 23 ± 2; Fig. 1a, Appendix S1: Fig. S3). Terrestrial ants in unflooded forest also exhibited the highest alpha diversity, as measured by the inverse Simpson index (forest type × stratum: $F_{3,24} = 32.82$, $P < 0.00001$, Fig. 1b). Whereas the diversity of terrestrial ants was significantly higher in unflooded than in flooded forest (Tukey's HSD, $P < 0.00001$), the diversity of arboreal ants was

not different between forest types (Tukey's HSD, $P = 0.1$, Fig. 1b).

Ant community structure varied by forest type and stratum (Fig. 1c, d; genus level, stratum $F_{1,24} = 24.21$, $P < 0.001$, forest type $F_{1,24} = 7.19$, $P < 0.002$; morphospecies level, stratum $F_{1,24} = 9.84$, $P < 0.001$, forest type $F_{1,24} = 4.92$, $P < 0.001$). Arboreal ant communities were more similar to one another between unflooded and flooded forest than terrestrial ant communities were (stratum × forest type, $F_{1,24} = 7.09$, $P < 0.001$,
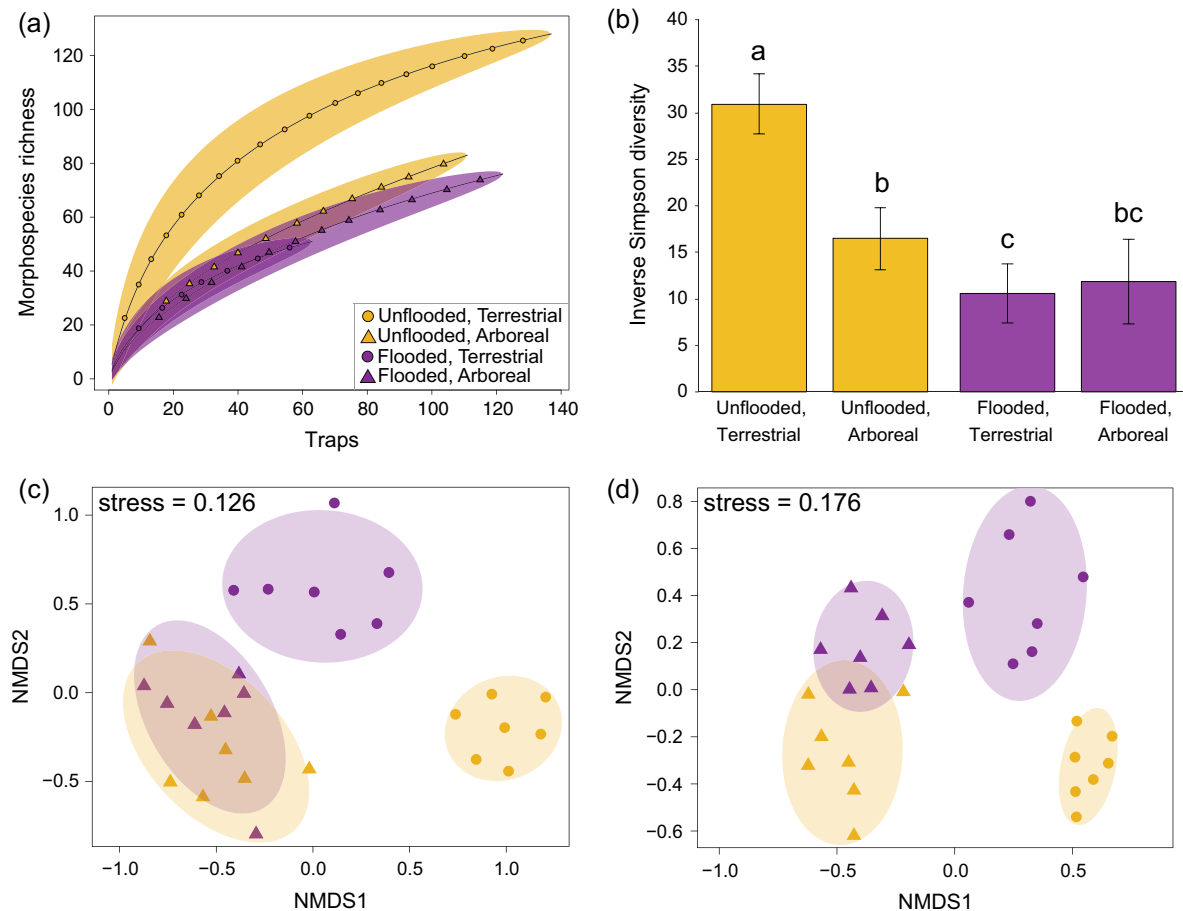

Fig. 1. Ant diversity in terrestrial and arboreal strata of unflooded and seasonally flooded forests. (a) Species accumulation curves of the expected mean species richness with 95% confidence intervals. (b) Diversities, calculated with inverse Simpson indices; bars show means and standard deviations per transect ($n = 7$). Different letters indicate diversity indices that are significantly different from one another by ANOVA and Tukey's post hoc tests ($P < 0.03$). (c, d) Ant community structure summarized by nonmetric multidimensional scaling (NMDS) analysis with Bray-Curtis dissimilarities at the (c) genus and (d) morphospecies levels. Shaded ellipses indicate 80% confidence intervals. Legend symbols in (a) apply to (a), (c), and (d). In all panels, yellow (grayscale, light gray) represents unflooded forest and purple (grayscale, dark gray) represents flooded forest.

$F_{1,24} = 4.09$, $P < 0.001$ at genus and morphospecies levels, respectively). The differences in terrestrial ant community structure between forest types were caused in part by the greater relative abundance of polydomous soil or litter dominants, including *Monomorium*, *Odontomachus*, *Wasmannia*, and *Pheidole*, in flooded forest, and the greater relative abundance of specialist litter predators, including *Strumigenys*, *Prionopelta*, and *Hylomyrma*, in unflooded forest (Appendix S3; see Delabie et al. 2005, Debout et al. 2007 for functional groups). Arboreal ants exhibited much more overlap in structure between unflooded and flooded forest at the genus level (Fig. 1c), with *Crematogaster*, *Camponotus*, and *Azteca* dominating both forest types.

Ant abundance and biomass

Terrestrial ants were more abundant in unflooded forest (Table 1; Appendix S1: Tables S2–S4), but, interestingly, and as we predicted, arboreal ants were more abundant in flooded forest (Table 1, Fig. 2, Appendix S1: Tables S5–S7). Estimates of ant colony abundance (occurrences) and of the total number of ant individuals (abundance) produced similar results (Table 1). Occurrences of ants from terrestrial traps in the dry season were significantly higher in unflooded than in flooded forest ($\chi^2 = 10.54$, $P < 0.002$; Table 1; Appendix S1: Table S2), and abundances were also marginally higher in unflooded than in flooded forest (raw data $\chi^2 = 3.35$, $P < 0.07$; Box-Cox transformed data $\chi^2 = 4.29$, $P < 0.04$; Appendix S1: Tables S3–S4). Conversely, arboreal ants exhibited marginally higher occurrences in flooded than in unflooded forest ($\chi^2 = 3.54$, $P < 0.06$; Table 1; Appendix S1: Table S5) and significantly higher abundances in flooded than in unflooded forest (raw data $\chi^2 = 7.26$, $P < 0.008$; Box-Cox transformed data $\chi^2 = 14.37$, $P < 0.0002$; Table 1; Appendix S1: Table S6–S7 and Fig. S4). Analysis of the Weibull distributions fit to arboreal ant abundance data also indicated that there were more arboreal ants in flooded forest: Abundances exhibited a higher scale parameter and a higher 75% quantile in flooded forest than in unflooded forest (Fig. 2c, d). Finally, arboreal ant biomass—approximated by the product of the average ant mesosomal length per trap and the corresponding number of ants—was also higher in flooded forest than in unflooded forest ($\chi^2 = 5.89$, $P < 0.02$; Table 1; Appendix S1: Table S8).

Trapping method and season also influenced ant abundance. Terrestrial ants were more abundant in Winkler traps than in ground pitfall traps

Table 1. Effect sizes for ant community data from generalized linear mixed models that included forest type as a potential fixed factor. The statistical comparisons represented here are within Forest type, Season, or Collection method.

| Response variable	Forest type		Season		Collection method		
	Unflooded	Flooded	Dry	High-water	Pitfall	Winkler	Beating
Terrestrial ant occurrence	5.7 ± 1.3*	3.3 ± 0.8*	N/A	N/A	4.0 ± 0.7*	9.1 ± 2.1*	N/A
Terrestrial ant abundance	19.2 ± 10.3†	9.9 ± 5.2†	N/A	N/A	11.7 ± 4.3*	64.9 ± 33.2*	N/A
Arboreal ant occurrence	2.5 ± 0.3†	2.9 ± 0.3†	2.8 ± 0.3	2.6 ± 0.3	2.0 ± 0.3*	N/A	3.3 ± 0.3*
Arboreal ant abundance	17.7 ± 9.6*	48.1 ± 25.5*	45.7 ± 21.9*	23.2 ± 11.0*	27.1 ± 11.6*	N/A	44.9 ± 19.2*
Arboreal ant mesosomal length ($\propto$ body size)	1.9 ± 0.3*	1.4 ± 0.3*	1.6 ± 0.3	1.7 ± 0.3	1.9 ± 0.3*	N/A	1.4 ± 0.2*
Arboreal ant PC1 traits	0.3 ± 0.2*	0.7 ± 0.2*	0.5 ± 0.2	0.5 ± 0.2	0.4 ± 0.1	N/A	0.6 ± 0.2
Arboreal ant body size × abundance ($\propto$ biomass)	29.0 ± 14.9*	73.4 ± 37.0*	68.7 ± 31.9*	31.1 ± 14.3*	17.7 ± 8.9*	N/A	86.2 ± 39.1*

*$P < 0.05$; †$P < 0.07$.
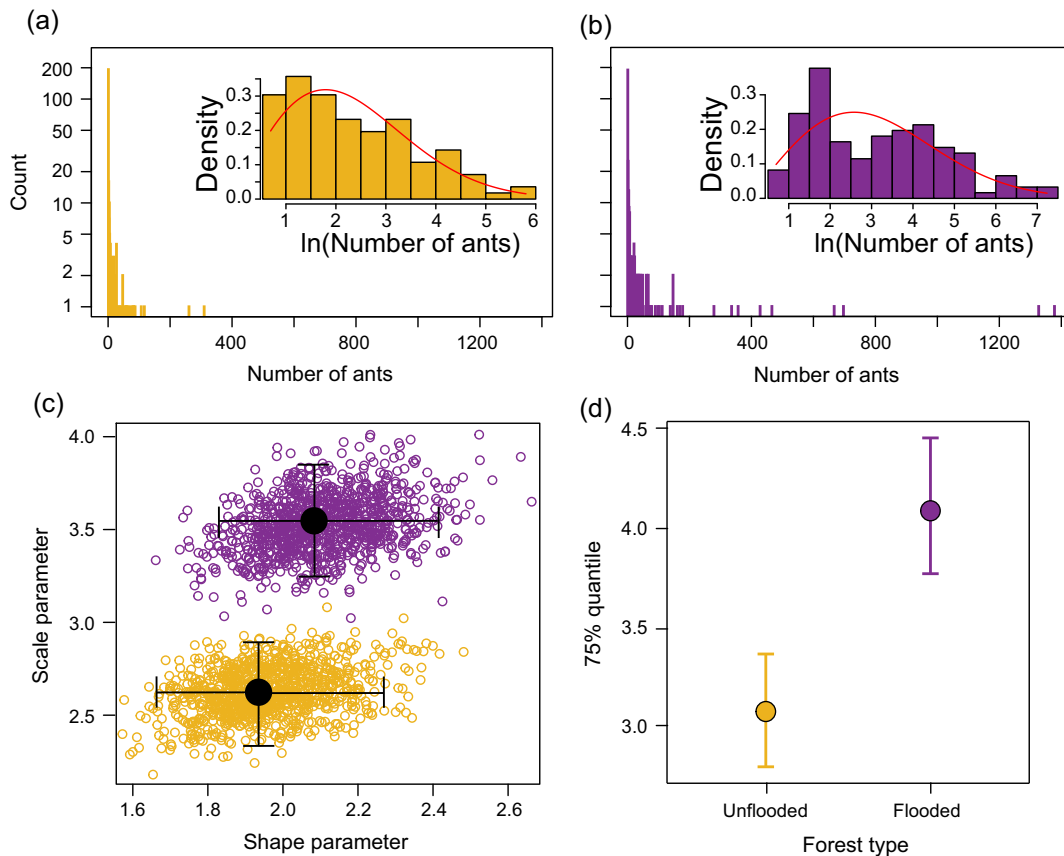
Fig. 2. Ant abundance in the arboreal stratum of unflooded and flooded forests. (a, b) Untransformed histograms and the respective log-transformed probability density functions of ant abundance per trap in (a) unflooded and (b) flooded forest. Red lines show the respective Weibull distribution fits to the log-transformed densities. (c) Bootstrapped values of the scale and shape parameters of the Weibull distributions fit to the log-transformed density functions shown in (a) and (b). (d) Bootstrapped values of the 75% quantile of the Weibull distributions. In both (c) and (d), filled circles show the median, and error bars represent the 95% confidence interval of the 1000 bootstrap replicates. In all panels, yellow (grayscale, light gray) represents unflooded forest and purple (grayscale, dark gray) represents flooded forest.

$(\chi^2 = 74.5, P < 0.0001)$. Arboreal ants were more abundant in vegetation-beating traps than in arboreal pitfall traps (raw data $\chi^2 = 109.76$, $P < 0.0001$) and in the dry season than in the rainy season in both forest types (raw data $\chi^2 = 21.06$, $P < 0.0001$). In unflooded forest, terrestrial ants were also more abundant in the dry season than in the rainy season (occurrence $\chi^2 = 15.39$, $P < 0.0001$; abundance $\chi^2 = 6.66$, $P < 0.01$; Appendix S1: Tables S9–S10).

Ant traits

Arboreal ant assemblages were on average smaller-bodied in flooded than in unflooded forest

$(\chi^2 = 12.9, P < 0.0004$, Fig. 3a) and also exhibited a smaller size range in flooded forest (standard deviation of ant mesosomal length per transect: flooded = 0.83 ± 0.28 mm, unflooded = 1.11 ± 0.26 mm; Wilcoxon test, $W = 148$, $P < 0.03$). These differences in average ant size between forest types were driven by changes in the species composition per trap (Fig. 1d). Linear mixed models showed that the effect of forest type on ant mesosomal length depended on season and collection method (Table 1; Appendix S1: Table S11): Ants were smaller in flooded than in unflooded forest in both seasons in vegetation-beating traps but only in the high-water season in arboreal pitfall
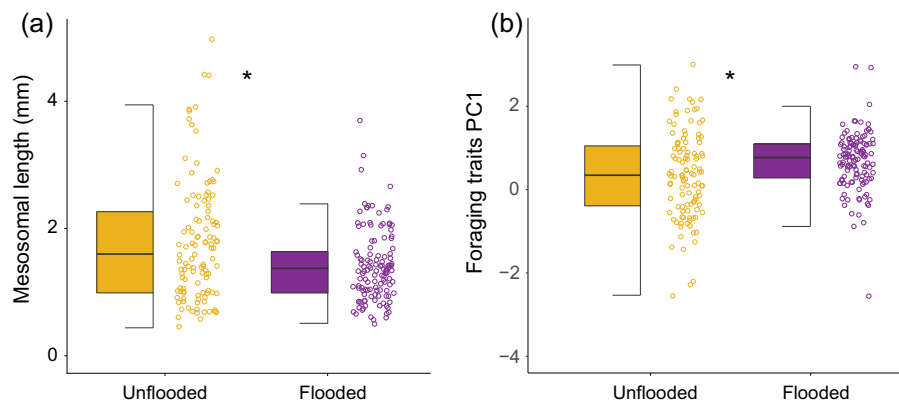
Fig. 3. Traits of arboreal ants in unflooded and flooded forests. (a) Mean mesosomal lengths—a proxy for ant body size—of morphospecies occurrences per trap; asterisk indicates $P < 0.0004$. (b) Mean values of the first principal component of foraging-related functional traits (i.e., head length, clypeus length, mandible length, petiole size, and distance from eyes to mandibular insertion, all standardized by ant body size) of morphospecies occurrences per trap; asterisk indicates $P < 0.003$. Boxes show median values and the 25th and 75th quantiles; whiskers extend a maximum of 1.5 times the range of the box. Points show scatterplots of the raw mean values in each trap. In both panels, yellow (grayscale, light gray) represents unflooded forest and purple (grayscale, dark gray) represents flooded forest.

traps (habitat × season × method: $\chi^2 = 12.16$, $P < 0.0005$).

Arboreal ants also exhibited a different morphological trait syndrome in flooded than in unflooded forest (Fig. 3b). In a principal component analysis, all five traits we chose for their putative relationships to ant foraging strategy loaded highly onto the first principal component (PC1 proportion of variance = 45%; loadings, head length = 0.53, clypeus length = 0.50, petiole size = −0.30, mandible length = 0.43, and eye-to-mandible distance = 0.44; Appendix S1: Tables S13, S14). Arboreal ants in flooded forest exhibited higher values of this first principal component than arboreal ants in unflooded forest ($\chi^2 = 9.39$, $P < 0.003$; Table 1; Appendix S1: Table S12), indicating that, on average, arboreal ants in flooded forest had longer clypei, longer heads, longer mandibles, longer eye-to-mandible distances, and smaller petioles than arboreal ants in unflooded forest (Fig. 3b). In addition, arboreal ants from flooded-forest traps exhibited less variation in these morphological traits than arboreal ants from unflooded forest (MANOVA $F_{1,68} = 4.86$, $P < 0.0008$; Appendix S1: Fig. S5).

Nitrogen isotopes ($\delta^{15}N$) suggested that ants feeding at lower trophic levels had longer clypei and higher values of the first principal component (PC1) of our morphological traits (Appendix S1: Fig. S6). Standard regressions for 35 genera showed a negative relationship between $\delta^{15}N$ and clypeus length (coefficient of clypeus length = −12.9 ± 6.0, $F_{1,33} = 4.64$, $P < 0.04$), but this relationship was not significant in a phylogenetic regression (coefficient of clypeus length = −8.5 ± 6.9, $F_{1,32} = 1.54$, $P = 0.2$). Clypeus length was the only trait with an individual relationship to $\delta^{15}N$ in our genus-level dataset. PC1 was negatively related to $\delta^{15}N$ only when we excluded *Strumigenys*, which had unusually long mandibles and high $\delta^{15}N$ ($F_{1,33} = 0.77$, $P = 0.4$ with *Strumigenys*; $F_{1,32} = 4.77$, $P < 0.04$ excluding *Strumigenys*), and this relationship was again nonsignificant when accounting for phylogeny. Both clypeus length and PC1 showed significant phylogenetic signal across the 35 analyzed genera (Blomberg's $K = 0.63$, $P < 0.003$, and $K = 0.82$, $P < 0.001$, respectively).

Plant communities

Forest type was associated with the predicted abundance of extrafloral nectar and myrmecophytic hemipterans. Stems in flooded forest were more likely to have extrafloral nectaries and/or myrmecophytic hemipterans than stems in unflooded forest ($\chi^2 = 7.35$, $P < 0.007$, Fig. 4).
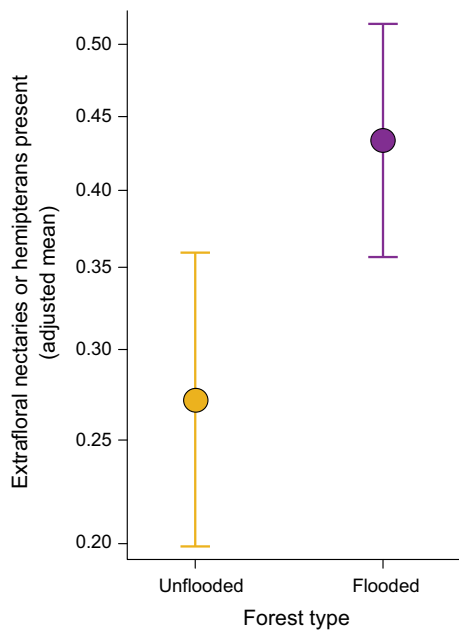
Fig. 4. Effect plot of the relative abundance of trees with extrafloral nectaries in unflooded and flooded forests. Adjusted means approximately correspond to the proportion of stems ≥10 cm dbh that are expected to have extrafloral nectaries or myrmecophytic hemipterans. Bars represent 95% confidence intervals.

Discussion

Ants are extraordinarily abundant in tropical rainforest canopies (Davidson et al. 2003). Here, we demonstrate that the productivity of Amazonian arboreal ants is positively related to that of the underlying forest. Consistent with our predictions, our three measures of arboreal ant productivity—occurrence, abundance, and estimated biomass—were all higher in seasonally flooded forest than in unflooded forest, consistent with the higher NPP of flooded forest in this system (Hawes et al. 2012, Hawes and Peres 2016). Our measures of ant productivity suggest that there were more arboreal ant colonies (i.e., occurrence was higher), which produced more workers (i.e., abundance was also higher), in flooded forest than in unflooded forest. Moreover, the difference in abundance was of sufficient magnitude that the estimated biomass of arboreal ants was higher in flooded forest than in unflooded forest, despite the smaller average body size of flooded-forest ants. The distinct compositions of ant communities in

arboreal and terrestrial strata indicated that flooded forest did not experience vertical compression of terrestrial species during the annual flood pulse. The discontinuity in the composition of the arboreal and terrestrial assemblages also suggested that the observed differences in abundance of arboreal ants between forest types were not driven by reduced resource competition between terrestrial and arboreal ants in flooded forest.

Few studies to date have addressed the relationship between secondary or tertiary productivity and primary productivity in tropical forests. We found a positive relationship between indicators of NPP and arboreal ant biomass, consistent with a global relationship (in which only two of 51 sites were tropical forests) between NPP and herbivore biomass (McNaughton et al. 1989). Yet our results thus also suggest that neither tree species richness nor aboveground tree biomass—both of which are lower in whitewater-flooded forest than in unflooded forest (Wittmann et al. 2006, Hawes et al. 2012)—is positively related to arboreal ant biomass in these forests, nor is arboreal ant biomass positively related to arboreal ant diversity. Productivity may in fact frequently be unrelated to species richness in unmanipulated systems (Adler et al. 2011). Arboreal ants exhibited several morphological traits that together were negatively related to $\partial^{15}N$ and suggested more herbivorous tendencies in flooded than in unflooded forest. The high productivity of ants in flooded forest may thus be driven by a greater availability of plant-derived resources. Mismatches between primary and secondary biomass can be caused by high turnover of primary production and/or by its stoichiometry: Population-level consumption of primary production is higher in high-nutrient environments, where plant food is more nutritious (Hillebrand et al. 2009). Arboreal ants, like strict herbivores (Urabe and Sterner 1996), may be tied stoichiometrically to primary producers in high-nutrient flooded forest.

Arboreal ants in flooded forest exhibited morphological traits suggestive of a more herbivorous foraging strategy than that of ants in unflooded forest. Flooded-forest arboreal ants were smaller and had higher values of a morphological principal component (PC1) indicating longer heads, longer clypei, longer eye-to-mandible distances, and smaller petioles relative to body size, all traits that have previously been

hypothesized to be related to herbivory (Parr et al. 2017). However, flooded-forest ants also had longer mandibles, a trait that has previously been associated with predation, but only among litter-nesting ant species (Silva and Brandão 2010). When excluding one particularly long-mandibled and predatory genus found primarily in terrestrial traps (*Strumigenys*), PC1 was also negatively related to generic $\partial^{15}N$, which suggests that the higher values of PC1 exhibited by flooded-forest arboreal ants may indeed indicate a lower average trophic level. The negative relationship that we detected between clypeus length alone and $\partial^{15}N$ is also notable. Although we do not know of another study that has examined this relationship explicitly, the insect morphological literature emphasizes that longer clypei support more developed cibarial musculature for sucking (Snodgrass 1935), as would be required for plant-exudate feeding by ants. Despite the trait–$\partial^{15}N$ relationships that we found via standard regressions, however, we did not detect phylogenetically corrected relationships. This may be because there were insufficient independent shifts toward herbivory within our genus-level phylogeny, or, alternatively, it may indicate that these traits are not in fact evolutionarily correlated. In addition, although previous studies have found that relative trophic positions among genera remain consistent across ecological contexts (Gibb and Cunningham 2011), our isotope analyses were generic averages from species collected beyond our study site, and these values might be site- and species-dependent. Future studies that incorporate species-level traits and phylogenies are warranted to clarify the functional significance of these traits to ant feeding strategy.

Our analysis of the predicted abundance of plant-derived food rewards, including extrafloral nectar and myrmecophytic honeydew-producing hemipterans, indicated a higher potential availability of such rewards in flooded forest. This higher predicted availability of plant exudates could support a higher biomass of more herbivorous arboreal ants and tie ant productivity to changes in primary productivity and chemistry. Precise characterization of the abundance of plant-based food rewards will require more information about these understudied Amazonian tree species. Resource differences between flooded

and unflooded forest could cascade up to arboreal ant biomass via at least four non-mutually exclusive pathways: (1) higher hemipteran biomass on high-nutrient growth (McNeill and Southwood 1978); (2) higher nutrients in tree or hemipteran exudates (Douglas 1993); (3) lower secondary metabolites in tree or hemipteran exudates (Pringle et al. 2014); and/or (4) higher carbohydrate availability caused by canopy heterogeneity (Ribeiro et al. 2013). Comparable data on hemipteran densities in these forests are necessary.

Most of the arboreal ants we collected in both forest types belong to genera or species that have been called "supreme tropical dominants" (Davidson 1997). Although only ~50% of the arboreal morphospecies were found in both flooded and unflooded forests, 17 of the 20 most abundant morphospecies in flooded forest were also found in unflooded forest and vice versa. Prominent among these were *Crematogaster* cf. *levior* and *Camponotus femoratus*, the parabiotic ants that form ant gardens—that is, arboreal carton nests that host epiphytes (Davidson 1988). Arboreal samples from fogging in Tambopata, Peru, were likewise numerically dominated by ant-garden species (Wilson 1987), suggesting broadscale consistency in arboreal ant communities across the Amazon basin. Davidson (1988) reported that ant gardens themselves were more abundant in the more frequently flooded areas of a supra-annually inundated whitewater-floodplain forest in Manu, Peru. Although that Peruvian forest floods less consistently and dramatically than várzea forests along the Juruá, similar mechanisms are probably at play. Moreover, our data build on the idea that ant gardens track light and the corresponding higher supply of carbohydrates into flooded habitats (Davidson 1988) to suggest that the productivity of entire arboreal ant communities is linked to the vigor of primary productivity across the Amazon basin.

Given the abundance and ecological importance of ants (Hölldobler and Wilson 1990), the differences that we found between flooded and unflooded forests could have profound functional consequences. Ants' voracious and frequently omnivorous appetites can structure entire food webs (Folgarait 1998). In the canopy, these appetites can feed back to affect the trees themselves, by reducing the abundances of other

animals, including both vertebrate and invertebrate herbivores (Davidson 1997). The environments that favor high abundances of ants in flooded forest are in contrast to the low-resource environments proposed to favor higher direct plant defenses—for example, toxic and fibrous leaves (Coley et al. 1985). We speculate that trees in whitewater-flooded forest could thus profitably tilt their defense investment toward ant biotic defenders (McKey 1984), a prospect that is consistent with the prevalence of ant rewards among pioneer trees (Heil and McKey 2003). Given that the density of individual ants per unit leaf area determines how likely they are to encounter and remove herbivores (Pringle et al. 2011), these feedbacks (i.e., trophic cascades) could be stronger in whitewater-flooded forest than in unflooded forest. Understanding how resources cascade up and down through tropical forest food webs could thus be critical to understanding net primary production itself.

Acknowledgments

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DATA AVAILABILITY

All supporting data and code have been deposited in the Dryad Digital Repository, https://doi.org/10.5061/dryad.dr1ms4v.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2902/full