Oecologia
https://doi.org/10.1007/s00442-018-4314-0

ECOSYSTEM ECOLOGY – ORIGINAL RESEARCH

Biogeochemistry and forest composition shape nesting patterns of a dominant canopy ant

Jelena Bujan[1,2] · **S. Joseph Wright**[3] · **Michael Kaspari**[2]

Received: 15 November 2017 / Accepted: 21 November 2018

Abstract

Humans are increasing nutrient deposition across the globe, and we know little about how these changes influence consumer populations in tropical rainforests. We used a long-term fertilization experiment conducted in a Panamanian forest to explore how nutrient availability and tree traits affect abundance of a higher-level consumer. We added nitrogen, phosphorus and potassium in a factorial design for 18 years. Given that phosphorus often limits ecosystem processes in lowland tropical forests, and added nitrogen reduces insect abundance in our experiment, we first hypothesized that phosphorus addition would increase nest density and nest size of *Azteca chartifex* ants while nitrogen addition would have the opposite effects. We found 48% lower nest density in the canopy of nitrogen addition plots relative to plots that did not receive nitrogen. Phosphorus addition did not affect nest density or size. These nutrient effects were not diminished by the selectivity of host trees. In general, larger trees held more nests, despite their low frequencies across the forest, while some abundant species (e.g., palms) were rarely used. We further predicted higher nest frequency on trees with extrafloral nectaries, because this ant fuels its large colonies with extrafloral nectar. Despite the non-random distribution of *A. chartifex* nests, across tree species and nutrient treatments, trees with extrafloral nectaries did not host more nests. Our study suggests that areas of a tropical lowland forest which are not oversaturated with nitrogen, and contain large trees, have higher nest density. This could enable *A. chartifex* in similar areas to outcompete other ants due to high abundance.

Keywords *Azteca trigona* · Neotropics · Nitrogen · Nest density · Nest size · Phosphorus

Introduction

Rapid changes of global nutrient availability caused by humans impact both plant and animal communities. Addition of a limiting nutrient to a forest, in general, promotes higher plant damage (Hargrove et al. 1984; Fox and Morrow 1992; Campo and Dirzo 2003; Andersen et al. 2010; Santiago et al. 2012) and increases the abundance of herbivores and predators (Forkner and Hunter 2000; Gruner and Taylor 2006). In highly diverse tropical rainforests, these anthropogenic impacts remain underexplored for consumer communities (Campo and Dirzo 2003; Gruner and Taylor 2006; Kaspari et al. 2017). Here, we tested how nutrient availability interacts with forest composition to affect the abundance of a dominant consumer.

Nitrogen (N) and phosphorus (P) are building blocks of macromolecules (Sterner and Elser 2002) and occur at relatively low densities in plant tissue compared to consumers (Mattson 1980; Elser et al. 2000; Denno and Fagan 2003; Matsumura et al. 2004). Both N and P have potentially wide ranging effects on consumer behavior (Toft and Wise 1999), trophic cascades (Mooney et al. 2010) and community structure (Hillebrand et al. 2007; Eskelinen et al. 2012). The weathered soils of lowland tropical forests are frequently P poor, especially relative to N that

---

Communicated by Andreas Prinzing.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00442-018-4314-0) contains supplementary material, which is available to authorized users.

✉ Jelena Bujan
jelena.bujan@ou.edu

[1] Department of Biology, University of Louisville, Louisville, KY 40292, USA

[2] Department of Biology, Graduate Program in Ecology and Evolutionary Biology, University of Oklahoma, Norman, OK 73019, USA

[3] Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Republic of Panama

accumulates in some lowland tropical forests through atmospheric deposition and biofixation (Vitousek and Sanford 1986; Vitousek 2004; Elser et al. 2007; Vitousek et al. 2010; Hietz et al. 2011). At the same time, increased N supplies can have negative effects, suppressing microbial and invertebrate diversity, and invertebrate abundance (Kaspari et al. 2017).

Ants are important terrestrial consumers whose colony size, both in terms of workers and reproductive individuals, increase with higher food quality (Aron et al. 2001; Portha et al. 2002; Kay et al. 2010). Relatively long colony lifespans in species like the dominant canopy ant *Azteca chartifex* make this taxonomic group useful as bioindicators of ecosystem change (Andersen et al. 2002). Moreover, the refuse produced by *A. chartifex* colonies increases decomposition, insect detrivory and predation in the litter under the nest (Clay et al. 2013), while also preventing tree colonization by some canopy ants (Adams et al. 2016). Because of its importance in shaping aboveground and belowground insect communities, we test two mutually compatible hypotheses regarding the role of biogeochemistry and forest composition on *A. chartifex* nest density and size: (1) the nutrient availability hypothesis and (2) the tree specificity hypothesis.

The nutrient availability hypothesis posits that adding a chemical element present at suboptimal levels will increase population survival and size. Thus, it predicts that higher foraging activity of *A. chartifex* which was recorded after chronic P addition in a long-term fertilization experiment on the Gigante Fertilization Plots (GFP; Bujan et al. 2016) is caused by increased nest density and size. Nitrogen addition on GFP decreased richness and abundance of litter arthropods (Kaspari et al. 2017). In general, anthropogenic influence over the past century increased N availability in the forests of this region, as seen in a nearby forest on Barro Colorado Island (Hietz et al. 2011). Thus, by adding such a plentiful nutrient, we predict a similar negative effect of this eutrophication and a decrease in nest density and nest size of this dominant ant. We used nest size as a proxy for colony size, because bigger nests, in other ant species, have been shown to belong to older and bigger colonies (Gordon and Kulig 1996; Tschinkel 2015). This allowed us to disentangle if differences in nest size and consequently colony growth are affected by long-term fertilization or the size of the host tree. We further predict that *A. chartifex* recruitment and numerical dominance at baits will be higher on N plots, if those ants are resource deprived. Dominant canopy ants select high-quality resources, a behavior which fosters territoriality and leads to resource monopolization (Blüthgen and Fiedler 2004). Resource deprived ants are predicted to recruit faster and to larger distances from the nest, which should result in higher recruitment and wider foraging ranges on N plots. We predict the opposite for nests found on P plots.

The tree specificity hypothesis predicts that tree characteristics impact nest density and nest size of *A. chartifex*. We first examine if some tree species are disproportionately used as nest sites, because plant species differ in resources supplied to insects and their effects on insect communities (Poelman et al. 2008). Consumption of resources important to *A. chartifex,* such as extrafloral nectar secretions and honeydew (Blüthgen et al. 2000; Weber and Keeler 2013) can directly increase fitness (Byk and Del-Claro 2011) and abundance of dominant ants (Blüthgen and Stork 2007). We predict that larger trees will support bigger nests, as larger trees contain higher ant richness (Klimes et al. 2012; Adams et al. 2016) and some provide higher herbivore abundance (Campos et al. 2006). *A. chartifex* colonies consist of spatially dispersed nests which can be placed at different locations in the canopy (Longino 2007). Such polydomous species, build their nests close to a stable resource (Holway and Case 2000; Lanan et al. 2011). Thus, we test if trees that provide extrafloral nectar resources hold higher nest frequency. Likewise, we predict that resource-poor trees will not be used as nest sites. Alternatively, the presence of extrafloral nectar could have a limited importance for nest placement of *A. chartifex* as has been shown for other non-mutualistic canopy ants (Camarota et al. 2015).

To test how biogeochemistry, tree size distributions and tree species composition shape the nest distribution and ant activity in a lowland tropical forest, we tested the impact of bottom–up regulation on nest density using abiotic (nutrients), and biotic requirements (tree characteristics). Understanding the effect of biogeochemical makeup on consumers is important, as shifts in density of the most dominant canopy consumer may alter the strength of trophic interactions across the forest. These shifts not only affect ant community structure but also are likely to impact the food web affecting both higher trophic levels, e.g., predation by large mammals, or lower trophic levels by altering herbivore abundance.

Materials and methods

We censused *Azteca* cf. *chartifex* nests in lowland moist forest in the Gigante Fertilization Experiment (GFP: 9°06′31″N, 79°50′37″W) within the Barro Colorado Nature Monument, Republic of Panama. Two species groups of *Azteca*, *Azteca* cf. *chartifex* and *Azteca* cf. *trigona*, build pendulous carton nests in Panamanian forests. Colonies across GFP belong to *Azteca chartifex* complex (D. Donoso, in prep), henceforth *A. chartifex*. These colonies are polydomous; so, we refer to them as nests throughout because we do not know which nest belongs to which colony. During July 2015, JB recorded each nest across 32 plots (40 × 40 m) fertilized with N, P and potassium (K) in a factorial design beginning in 1998. Each of the treatments (+N, +P, +K, +NK, +NP, +PK, +NPK) is replicated four times, including the controls. These four replicates accounted for spatial variation in soils (Yavitt et al. 2009) and tree composition associated with a slight topographic gradient (SJW, unpublished data). Two blocks were nested within every replicate one consisting of N, P, K and NPK treatments, and the other included NP, NP, PK and control (for details see Wright et al. 2011). Nest counts were not done at time zero, 18 years prior to this study. Although *A. chartifex* colonies can be long-lived—which potentially suggests nesting patterns will reflect inherent differences within the forest—we expect a turnover in colony size during almost two decades. Colony size can increase with both additions of new nests and increases in size of old nests and is more likely in colonies with sufficient resources. Thus, to understand *Azteca* nesting patterns, we test for differences associated with forest composition and with our nutrient treatmets.

Nest density

To test for differences in nest density across fertilization treatments, we visually inspected the canopy of each plot for the presence of *A. chartifex* nests. If the canopy was particularly dense, we used binoculars. We started at the south edge of the plot and walked in a straight line to the north edge stopping every five meters to inspect the canopy above. After reaching the plot edge, we moved five meters east and applied the same procedure walking southwards. In total, we had 81 inspection points at each plot. When we located a nest, we marked its location with a GPS (Garmin GPSMAP 64 s) and assigned a unique identifying number. We inspected 32 plots (four replicates of the eight treatments in the factorial NPK experiment) comprising an area of 5.12 ha. We tested for difference in nest density across the plots with generalized linear models (GLMs) with a 'glm' function in R (R Core Team 2016). We used N, P, K, their interactions, and blocks nested within replicates as main effects. To select the optimal model, we used Information Theoretic approach (Burnham and Anderson 2003). After constructing our models, we ran a model comparison based on ΔAIC values—the difference of the AIC of the *i*th model and the model with the lowest AIC value.

Nest size

We measured nest length and height using a Laser Distance Meter (Leica Disto D5) affixed on a tripod. We recorded three distances (Fig. 1a): first, to the top of the nest (a), bottom of the nest (b), and the distance to the ground (d). We also recorded two angles: one between the nest top and bottom (α), and the other between the nest top the ground (β). This allowed us to calculate nest length (l) and the height of the nest in the canopy (h). Lastly, we took a nest photo at the same location where all the measurements were taken.

We calculated the nest length and height from our nest measurements (Fig. 1A), as the side in an irregular triangle: $l^2 = a^2 + b^2 - 2a \times b \times \cos(\alpha)$. Using the photo of the nest and Image J software, we measured the nest length in pixels which allowed us to calculate the diameter of the nest and, to calculate the approximate nest volume. We sorted the nests in three shape categories: prolate spheroid (Fig. 1B), cone (Fig. 1C), cylinder (Fig. 1D) and we used appropriate formula to calculate the volumes of these shapes (Hillebrand et al. 1999; Sun and Liu 2003). Nest volume was an estimate of nest size, which is, in other ants, positively correlated with colony size and worker size (Tschinkel 2015). We were unable to accurately measure the smallest nests (<0.5 L) with the laser, so they were excluded from our analyses. However, those were usually satellite nests around the main nest and their addition is unlikely to significantly change the nest size analysis.

To test for size differences, we performed generalized linear models (GLMs) with N, P, K, their interactions, DBH, and block nested within replicate as main effects. DBH was added to this model, because exploration showed a positive correlation between tree size and nest size. Nest volumes were square root transformed prior to the analyses to normalize the data.

Recruitment and dominance at baits

To study *A. chartifex* recruitment and dominance at baits, we focused on N and P fertilizations and controls. We selected N as it decreases invertebrate abundance and diversity (Kaspari et al. 2017), while P increases *A. chartifex* activity (Bujan et al. 2016). To test if *A. chartifex* bait recruitment is affected by the vicinity of the nest as well as nest size and height, we used a set of 11 baits. We established our baiting transects with the tree hosting the nest, and baited understory vegetation every 0.5–1 m at eye level. We set up the transect around the highest vegetation density around the nest, as these ants are known to use lianas as walkways (Yanoviak 2015). We chose the nests which were surrounded with lianas, so that the ants can access the baits easily from the canopy. We used mixed tuna with honey as our bait because it provides protein, carbohydrates, lipids and salt. We recorded the number of ants present at baits after 5 min (recruitment) and 1 h (dominance) with respect to the vicinity of the nest, using a base 2 logarithmic scale (i.e., 1, 2, 4, 8, 16, 32, …). We baited 12 nests from control and P plots, and 7 nests from N treatments as the number of nests was low on N plots. At the beginning and the end of each baiting transect, we measured air temperature by aiming an IR thermometer (Fluke Corporation, Everett, WA; model 62) at eye level to a shaded spot >10 m away.

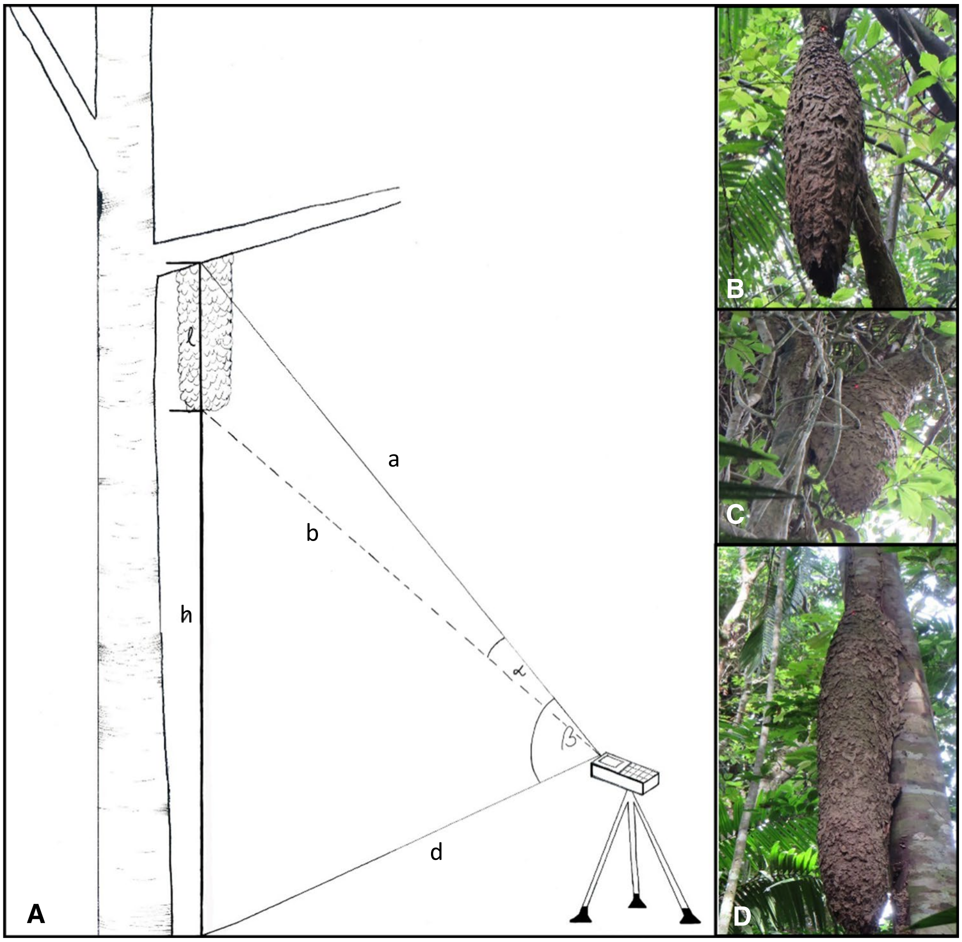

Fig. 1 Diagram depicting measures for nest height and length of the *Azteca chartifex* nest (**A**). We measured three distances: (a) to the top of the nest, (b) to the bottom of the nest, and (d) the distance to the ground. We measured two angles: (α) between the nest top and bottom, and (β) between the nest top the ground. This allowed us to calculate nest length (l) and nest height in the canopy (h). Nest images are examples of three shape categories we used: prolate spheroid (**B**), cone (**C**), and cylinder (**D**)

We examined recruitment rate and numerical dominance at baits placed at three different distances from the nest: (1) at the host tree, (2) at the baits within 5 m (sum of ant abundance at baits 1–5) and (3) at 6–10 m (sum of ant abundance at baits 6–10) from the host tree. For both recruitment and dominance at baits, we used full ANCOVA models using nutrient treatments: N, P, average temperature, nest characteristics (height and volume), and plot identity to control for spatial variation. Foraging range of *A. chartifex* often exceeds 10 m, and their foraging area is a viciously defended territory whose size depends on colony size (Adams 1990). Therefore, we use nest size in our analyses to account for differences in foraging distance caused by nest size.

Tree traits

We recorded the size of the plant hosting the nest and the growth form (tree or liana). If the tree was > 10 cm in diameter at breast height (DBH), then we used the identifications and measurements from the 2013 GFP tree census (Wright et al. 2018). To test for the *Azteca* nest occurrence across different tree species, we first calculated the actual frequency of each tree species across all plots, and then compared those with the observed nest frequencies using a Chi-square test, a frequently used approach in testing the nesting preferences (Thomas and Taylor 1990).

To test if *Azteca* nests occur more frequently on trees bearing extrafloral nectaries (EFN), we focused on tree species where we recorded at least one nest. We searched the literature to see if the species was found to produce EFN in Panama (Croat 1978; Schupp and Feener 1991; Goitía and Jaffe 2009; Bixenmann et al. 2011). We restricted our search to EFN, since it is not clear that all small bodies produced by tree species are used by ants (Schupp and Feener 1991). We compared the number of nests on trees with and without EFN to the Kruskal–Wallis test. All analyses were performed in R version 3.3.2 (R Core Team 2016).

Results

Effect of fertilization on nest density

We recorded a total of 200 nests across all fertilization plots, with an average nest density of 39 nests/ha. Across eight different treatments, the lowest number of nests was found on

+N plots (mean ± SE: 2.5 ± 1.0 nests/plot) while the nests were on average most abundant on control plots (11.0 ± 2.0 nests/plot). Nitrogen addition decreased nest density compared to the plots which did not receive N (Table 1). Three GLMs were within 2 AIC units of the lowest AIC value and were, therefore, used to analyze the effects of nutrients on *Azteca* nest density (Table 1). These three models would be expected to be optimal models in 71% of cases (Akaike Weights, Table 1). Nest density was on average 48% lower across N plots (i.e. +N, +NK, +NP, +NPK; $n = 16$; 4.3 ± 0.9 nests; Fig. 2, Table 1) compared to the plots which did not receive N (i.e., CTR, +P, +K, +PK; $n = 16$; 8.2 ± 0.8 nests). Number of nests was also significantly lower when N was added together with P (i.e. +NP, +NPK; $n = 8$; 6.0 ± 1.3 nests; Fig. 2, Table 1).

Effect of fertilization on nest size

We measured 169 *A. chartifex* nests ranging from 0.21 to 2.61 m in length (mean ± SE 0.93 ± 0.04 m), with volumes ranging from 1.2 to 289.0 L (mean ± SE 53.8 ± 4.2 L). Optimal model accounting for variation in nest size contained two significant model terms tree size (DBH) and block nested within replicate, but none of the added nutrients (Table 2). Larger trees, and trees located in the northeast, less palm-dominated part of GFP, on average contained larger nests (Replicate 4, Fig. 3).

Azteca recruitment rate and dominance

Within the 5 m closest to the host tree ants recruited faster only if their nest was lower in the canopy, as the abundance at baits was positively correlated with nest height (Table S1A; ANCOVA: $F_{1,23} = 5.3$, $p = 0.03$). We recorded the same pattern with ant dominance at baits, after 1 h, as the best predictor of abundance at baits within 5 m was the nest height (Table S1B; ANCOVA: $F_{1,22} = 9.3$, $p = 0.006$). Ants were recruiting equally fast to baits on the host tree across studied treatments and the same was true for baits 6–10 m away from the host tree. Recruitment rate or dominance was not significantly affected by the two nutrients examined (N and P), the nest size, the plot at which they were collected, or the temperature at which ants were foraging (Table S1).

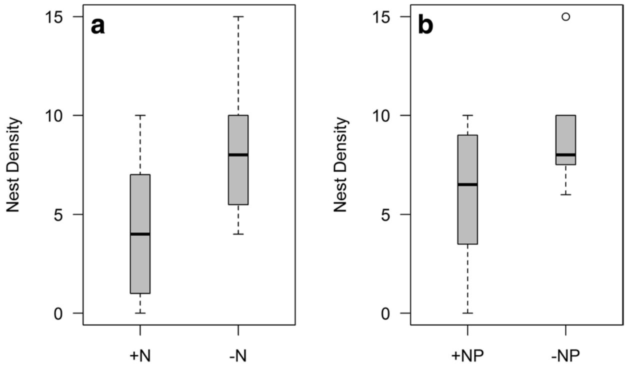

Fig. 2 Treatments in which *Azteca chartifex* nest density differed significantly. **a** Plots that received nitrogen addition +N (+N, +NK, +NP, +NPK), and plots were not fertilized with N (−N: control, P, K, PK); **b** plots which received both nitrogen and phosphorus addition +NP (+NP, +NPK) compared to plots which did not received those nutrients (−NP: control, K)

Nesting sites are tree specific

Azteca chartifex nested on 41 of the 249 tree species (17%) recorded for the 32 fertilization plots. We found a non-random distribution of *A. chartifex* nests across these species [χ^2 (1) = 2437.8, $p < 0.001$]. The highest number of nests was recorded on *Heisteria concinna* (12%) and *Tetragastris panamensis* (11%). Some tree species were frequently chosen as nest sites despite their low frequency across the plots, including: *Prioria copaifera*, *Drypetes standleyi*, and *Trattinnickia guianense*. In contrast, the palm *Oenocarpus*

Table 1 Generalized linear models used to test the nest density across fertilization plots

Model	*df*	AIC	ΔAIC	w_i
***N* + *N* × *P* + REPL**	**5**	**168.27**	**0.00**	**0.34**
N* + *N* × *P	**4**	**169.23**	**0.97**	**0.21**
***N* + *N* × *P* + REPL + REPL × BLOCK**	**6**	**169.74**	**1.48**	**0.16**
N + P + *N* × *P* + REPL + REPL × BLOCK	7	170.61	2.35	0.11
N + P + *N* × *P* + P × K + REPL + REPL × BLOCK	8	171.44	3.17	0.07
N	3	172.25	3.98	0.05
N + P + K + *N* × *P* + P × K + REPL + REPL × BLOCK	9	172.60	4.33	0.04
N + P + K + *N* × *P* + N × K + P × K + REPL + REPL × BLOCK	10	173.75	5.49	0.02
Null	2	180.52	12.26	0.00

For each model degrees of freedom, AIC values, ΔAIC (difference between the *i*th model and the model with the lowest AIC), and Akaike weights (w_i) are listed. Models within 2 AIC from the optimal model with the lowest AIC value are listed in bold. Treatments in italic indicate significance ($\alpha = 0.05$)

Table 2 Generalized linear models used to test variation in nest volume across the fertilization plots

Model	DF	AIC	ΔAIC	w_i
REPL × BLOCK + DBH	**4**	**688.35**	**0.00**	**0.54**
REPL + REPL × BLOCK + *DBH*	**5**	**690.30**	**1.95**	**0.20**
N + K + REPL + REPL × BLOCK + *DBH*	7	691.80	3.45	0.10
N + REPL + REPL × BLOCK + *DBH*	6	692.29	3.93	0.08
N + P + K + REPL + REPL × BLOCK + *DBH*	8	693.36	5.01	0.04
N + P + K + N × K + REPL + REPL × BLOCK + *DBH*	9	694.23	5.87	0.03
N + P + K + N × P + N × K + REPL + REPL × BLOCK + *DBH*	10	695.96	7.60	0.01
N + P + K + N × P + N × K + P × K + REPL + REPL × BLOCK + *DBH*	11	697.85	9.49	0.01
DBH	3	701.70	13.35	0.00

For each model degrees of freedom, AIC values, ΔAIC (difference between the *i*th model and the model with the lowest AIC), and Akaike weights (w_i) are listed. Models within 2 AIC from the optimal model with the lowest AIC value are listed in bold. Treatments in italic indicate significance ($\alpha = 0.05$)

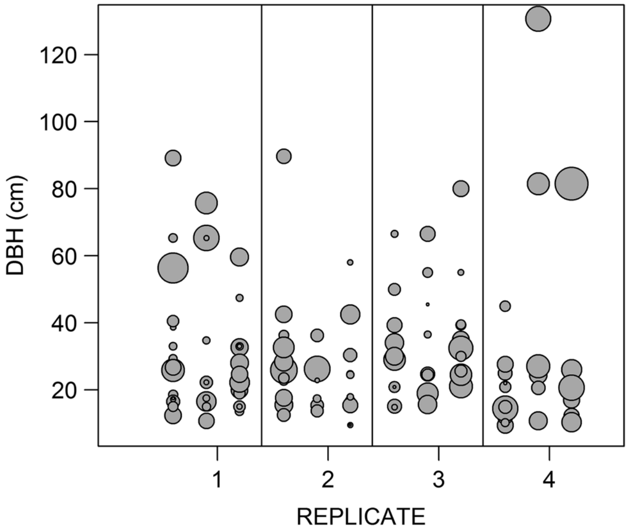

Fig. 3 Nest size across different areas of the forest (replicate), across trees of different diameter at breast height (DBH). Circle size corresponds to the nest volume, the nest size estimate. A categorical variable replicate (1–4) accounted for differences in topography and vegetation composition. The maximum elevational difference was 36 m, as there is a gentle slope going from the low lying southwest corner to the northeast corner of the study site. A gradient in the density of palm trees across the plots goes from less palm-covered (4) to lower, more palm-rich plots in the southwest (1)

mapora, the third most abundant tree across fertilization plots was almost never used; only 1% of the nests were recorded in its canopy. Despite the lower frequency of large trees across GFP, nests of *A. chartifex* were predominantly found on large trees (Fig. S1). In our experiment, this right-skewed distribution of tree sizes was recorded across all eight nutrient treatments (Fig. S2).

For 160 of our nests, we identified host tree species and assigned the presence or absence of EFN. We recorded only 17 nests in the canopy of trees with EFN (11%). Among the total tree species pool *Azteca* nest density was not higher on trees with extrafloral nectaries [Kruskal–Wallis, χ^2 (1) = 0.04, p = 0.85].

Discussion

Changes in biogeochemistry can impact consumers by increasing the food availability and quality, resulting in enhanced abundances of herbivores and predators (Haddad et al. 2000; Gruner 2004). Here, however, we found no evidence for increased nest density in *A. chartifex* after receiving a long-term N, P, K addition. To the contrary, N addition decreased nest density by 48%. This difference is more striking when only N addition and control plots are compared, as a single N addition had four times lower number of nests than the controls. In contrast, activity near the nests was invariant across the biogeochemical template.

Nest size was not affected by nutrient addition, but best predicted by tree size and location in the forest. We found higher nest density on certain tree species, despite their low occurrence in forest while others, such as the most abundant palm species, were rarely used as nest sites. The presence of EFN did not promote nest density. Our study suggests that *A. chartifex* nesting locations and densities are driven by nutrient availability and forest composition acting in concert to promote its dominance in this lowland tropical forest.

Low nest density on nitrogen plots

A working hypothesis in the geography of nutrient limitation states that P limitation supplants N limitation as one moves from the new soils of the Nearctic to the weathered soils of the Neotropics. In temperate forests, N fertilization increases the number of phloem feeders, and this could result in an increase of ants tending them (Strauss 1987). However, in the studied nutrient-rich tropical forest, N addition decreased arthropod abundance and richness (Kaspari et al. 2017).

We suggest that the lack of prey and honeydew producing mutualists could be one of the reasons why N plots tend to have lower nest density of *A. chartifex*. Furthermore, fertilization can alter the abundance of phloem feeders and the quality of the produced honeydew which affects ant-tending behavior (Gonthier et al. 2013). Some tree species might be used as nest sites more frequently if they have a higher herbivore load, and fertilization could promote herbivory in the canopy as it did in the understory of this forest (Santiago et al. 2012). It remains to be tested which of the fertilization treatments have a negative effect on phloem feeders and honeydew quality, and how that relates to changes in ant activity and nest density. Finally, one of the benefits of having multiple nests is increased resource acquisition through expansion of the foraging area (Debout et al. Debout et al. 2007). Such polydomous species can place nests close to stable resources (Holway and Case 2000, Lanan et al. 2011), which suggests that low nest density on N plots might be caused by low resource availability across those plots.

Recruitment and dominance are not affected by nutrients

We assumed that higher ant abundance at the plot level after P fertilization (Bujan et al. 2016) could be driven by colony level requirements. If more resources are needed ants will: (1) recruit to the baits faster; (2) forage further away from the nest, and (3) dominate the resources (higher abundance). What we found instead is that the proximity of the nest is the main driver of both ant recruitment and dominance. Recruitment of *A. chartifex* might not be affected by nest size or the addition of N or P because of the territoriality of this species which places guardian workers across its territory and we conservatively sampled the closest 10 m (Adams 1990). Thus, overall higher foraging activity recorded on P plots is due to a joint effect of the nest height in the canopy and high nest density, compared to low nest density across N fertilization.

Azteca frequently nests on certain trees

We found that larger trees hosted more nests, despite their low frequency in the forest (Fig. S1), and canopies of large trees also supported bigger nests (Fig. 3). Tree characteristics have been proposed to shape canopy ant mosaics (Sanders et al. 2007); so, we explored those traits shared by tree species which were both less abundant in the forest and frequently selected as nesting sites: *Prioria copaifera*, *Drypetes standleyi*, and *Trattinnickia guianense*. These species belong to separate families: Fabaceae, Euphorbiaceae, Burseraceae, respectively, and as such they have very different flowering and fruiting patterns, as well as the bark structure (Croat 1978; Condit et al. 2010). None of these species produce extrafloral nectar in Panama (Schupp and Feener 1991), but all are particularly high canopy trees with average heights 28–30 m (SJW, unpublished data). This could be one of the reasons why the nests are more commonly found on those trees, regardless of their low frequency in the forest. Nests in the tallest canopy trees may deter the attacks of tamandua anteaters that can destroy nests with their long claws as they feed on *Azteca* larvae (Lubin et al. 1977), especially if these trees are not well connected with lianas.

Nests were rarely recorded on other abundant tree species, such as palm *Oenocarpus mapora*. We observed only three nests on palms, and they were generally smaller nests (mean ± SE 14.8 ± 10.1 L). Palms in this forest are mostly understory trees, they have smaller canopy, rarely colonized by lianas, and as such are disconnected from the rest of the canopy. Canopy ants rely on resources in the canopy of the host tree but they use lianas walkways to access other canopies (Clay et al. 2010; Yanoviak 2015) and as a source of extrafloral and honeydew secretions (Blüthgen and Fiedler 2002). Thus, palm canopies could be too isolated, and too small to alone provide sufficient resources for *A. chartifex* colonies, in contrast to tall canopy trees. These mechanisms remain to be tested.

Contrary to our prediction, we found no bias toward species bearing extrafloral nectaries. This could be because tree species from genera that produce extrafloral nectar, such as *Inga* (Bixenmann et al. 2011), while abundant across the forest, never host *A. chartifex* nests due to their small size. *Inga* was the most specious genus found across the plots represented with 9 species, all of which produce extrafloral nectaries (Croat 1978; Goitia and Jaffe 2009; Bixenmann et al. 2011) and none of these species hosted a single nest. The presence of extrafloral nectaries, and their activity, was not important for structuring in an ant community of the Brasilian Cerrado (Camarota et al. 2015) suggesting that, in general, for non-mutualistic canopy ants, extrafloral nectar has limited importance.

Caveats

Due to the logistical constraints, it would be almost impossible to measure plant secretions across the canopies of the fertilization experiment and the abundance of phloem feeders. To directly test if hemiptera abundance changed with fertilization and the effect on the *A. chartifex* nesting patterns, targeted canopy fogging would be one of the most reliable sampling methods. Fogging would also provide insight on arthropod prey abundance in the canopy, where these ants mostly forage to test if N-plot canopies have reduced prey abundance as found in the leaf litter (Kaspari et al. 2017). Such destructive sampling was not possible within this long-term fertilization experiment. Lastly, examining canopy connectivity by measuring liana abundance across the plots would provide a test if higher liana load on N plots enables higher tamandua predation.

Outlook

To our knowledge, this is the first study addressing the effect of biogeochemistry and forest composition on nesting patterns of a dominant consumer. We show that the addition of N, in a nutrient-rich lowland tropical forest, halves the number of *A. chartifex* nests. This suggests that biogeochemistry impacts habitat usage of a dominant canopy consumer, and it remains to be tested if this bottom–up effect scales up to other arthropods. We also found that nest site distribution is non-random, and that *A. chartifex* more frequently nests in large canopy trees. Dominant ant species compete with each other for foraging area, creating a patchwork, or a mosaic, of territories in agricultural systems (Room 1971; Majer 1976). The presence of dominant ant species in nature could shape the ant mosaic in the canopy by excluding other ants (Adams et al. 2016; Camarota et al. 2016), also impacting other arthropods in those trees. The density and the locations of *A. chartifex* nests alter the abundance of both canopy and understory arthropods, and with the refuse production each nest further elevates nutrient concentrations in the litter (Clay et al. 2013). Additionally, predation patterns might change with altered biogeochemistry, as *A. chartifex* larvae are common food for tamanduas (Lubin et al. 1977), so tamanduas might target high nest densities areas. To fully understand ecosystem responses to nutrient alterations we need more studies focusing on the response of higher level consumers. Anthropogenic alterations of nutrient availability will affect consumer communities across the globe, and we just begun exploring these effects.

Acknowledgements Comments of Michael Patten, Ellen Welti, Lara Souza and Ana Ješovnik as well as suggestions of two anonymous reviewers and the handling editor greatly improved our manuscript. Oris Acevedo and Belkys Jimenez of the Smithsonian Tropical Research Institute provided logistical support in Panama. Arthur Escalas provided valuable R advice. This study was funded by the Biology Department (OU), the Graduate Student Senate (OU), and Frankopan Fund Fellowship awarded to JB, and National Science Foundation Macrosystems Grant EF-1065844 awarded to MK. The experiments in this study comply with the current laws of the Republic of Panama.

Author contribution statement SJW designed and conducted the long-term fertilization experiment. JB, MK and SJW conceived and designed the study. JB conducted field work, analyzed the data and wrote the manuscript. MK and SJW provided editorial advice.

References

Adams ES (1990) Boundary disputes in the territorial ant *Azteca trigona*: effects of asymmetries in colony size. Anim Behav 39:321–328. https://doi.org/10.1016/S0003-3472(05)80877-2

Adams BJ, Schnitzer SA, Yanoviak SP (2016) Trees as islands: canopy ant species richness increases with the size of liana-free trees in a Neotropical forest. Ecography (Cop) 39:1–9. https://doi.org/10.1111/ecog.02608

Andersen AN, Hoffmann BD, Muller WJ, Griffiths AD (2002) Using ants as bioindicators in land management: simplifyings assessment of ant community responses. J Appl Ecol 39:8–17. https://doi.org/10.1046/j.1365-2664.2002.00704.x

Andersen KM, Corre MD, Turner BL, Dalling JW (2010) Plant-soil associations in a lower montane tropical forest: physiological acclimation and herbivore-mediated responses to nitrogen addition. Funct Ecol 24:1171–1180. https://doi.org/10.1111/j.1365-2435.2010.01731.x

Aron S, Keller L, Passera L (2001) Role of resource availability on sex, caste and reproductive allocation ratio in the Argentine ant Linepthema humile. J Anim Ecol 70:831–839

Bixenmann RJ, Coley PD, Kursar TA (2011) Is extrafloral nectar production induced by herbivores or ants in a tropical facultative ant-plant mutualism? Oecologia 165:417–425. https://doi.org/10.1007/s00442-010-1787-x

Blüthgen N, Fiedler K (2002) Interactions between weaver ants Oecophylla smaragdina, homopterans, trees and lianas in an Australian rain forest canopy. J Anim Ecol 71:793–801. https://doi.org/10.1046/j.1365-2656.2

Blüthgen N, Fiedler K (2004) Competition for composition: lessons from nectar-feeding ant communities. Ecology 85:1479–1485

Blüthgen N, Stork N (2007) Ant mosaics in a tropical rainforest in Australia and elsewhere: a critical review. Aust Ecol 32:93–104

Blüthgen N, Verhaagh M, Goitía W et al (2000) How plants shape the ant community in the Amazonian rainforest canopy: the key role of extrafloral nectaries and homopteran honeydew. Oecologia 125:229–240. https://doi.org/10.1007/s004420000449

Bujan J, Wright SJ, Kaspari M (2016) Biogeochemical drivers of Neotropical ant activity and diversity. Ecosphere 7:e01597. https://doi.org/10.1002/ecs2.1597

Burnham KP, Anderson DR (2003) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York

Byk J, Del-Claro K (2011) Ant-plant interaction in the Neotropical savanna: direct beneficial effects of extrafloral nectar on ant colony fitness. Popul Ecol 53:327–332. https://doi.org/10.1007/s10144-010-0240-7

Camarota F, Powell S, Vasconcelos HL et al (2015) Extrafloral nectaries have a limited effect on the structure of arboreal ant communities in a neotropical savanna. Ecology 96:231–240. https://doi.org/10.1890/14-0264.1

Camarota F, Powell S, Melo AS et al (2016) Co-occurrence patterns in a diverse arboreal ant community are explained more by competition than habitat requirements. Ecol Evol 6:8907–8918. https://doi.org/10.1002/ece3.2606

Campo J, Dirzo R (2003) Leaf quality and herbivory responses to soil nutrient addition in secondary tropical dry forests of Yucatán, Mexico. J Trop Ecol 19:525–530. https://doi.org/10.1017/S0266467403003572

Campos RI, Vasconcelos HL, Ribeiro SP et al (2006) Relationship between tree size and insect assemblages associated with Anadenanthera macrocarpa. Ecography (Cop) 29:442–450. https://doi.org/10.1111/j.2006.0906-7590.04520.x

Clay NA, Bauer M, Solis M, Yanoviak SP (2010) Arboreal substrates influence foraging in tropical ants. Ecol Entomol 35:417–423. https://doi.org/10.1111/j.1365-2311.2010.01197.x

Clay NA, Lucas J, Kaspari M, Kay AD (2013) Manna from heaven: refuse from an arboreal ant links aboveground and belowground processes in a lowland tropical forest. Ecosphere 4:art141. https://doi.org/10.1890/es13-00220.1

Condit R, Pérez R, Daguerre N (2010) Trees of Panama and Costa Rica. Princeton University Press, Princeton

Croat TB (1978) Flora of Barro Colorado Island. Stanford University Press, Palo Alto

Debout G, Schatz B, Elias M, Mckey D (2007) Polydomy in ants: what we know, what we think we know, and what remains to be done. Biol J Linn Soc 90:319–348. https://doi.org/10.1111/j.1095-8312.2007.00728.x

Denno R, Fagan WF (2003) Might nitrogen limitation promote omnivory among carnivorous arthropods? Ecology 84:2522–2531

Elser JJ, Sterner RW, Gorokhova E et al (2000) Biological stoichiometry from genes to ecosystems. Ecol Lett 3:540–550

Elser JJ, Bracken MES, Cleland EE et al (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol Lett 10:1135–1142. https://doi.org/10.1111/j.1461-0248.2007.01113.x

Eskelinen A, Harrison S, Tuomi M (2012) Plant traits mediate consumer and nutrient control on plant community productivity and diversity. Ecology 93:2705–2718

Forkner RE, Hunter MD (2000) What goes up must come down? Nutrient addition and predation pressure on Oak Herbivores. Ecology 81:1588. https://doi.org/10.2307/177309

Fox L, Morrow P (1992) Eucalypt responses to fertilization and reduced herbivory. Oecologia 89:214–222

Goitía W, Jaffe K (2009) Ant-plant associations in different forests in Venezuela. Neotrop Entomol 38:1–42

Gonthier DJ, Ennis KK, Philpott SM, Vandermeer J, Perfecto I (2013) Ants defend coffee from berry borer colonization. Biocontrol 58(6):815–820

Gordon DM, Kulig AW (1996) Founding, foraging, and fighting: colony size and the spatial distribution of harvester ant nests. Ecology 77:2393–2409

Gruner DS (2004) Attenuation of top-down and bottom-up forces in a complex terrestrial community. Ecology 85:3010–3022

Gruner DS, Taylor AD (2006) Richness and species composition of arboreal arthropods affected by nutrients and predators: a press experiment. Oecologia 147:714–724. https://doi.org/10.1007/s00442-005-0337-4

Haddad NM, Haarstad J, Tilman D (2000) The effects of long-term nitrogen loading on grassland insect communities. Oecologia 124:73–84. https://doi.org/10.1007/s004420050026

Hargrove W, DA Crossley J, Seastedt T (1984) Shifts in insect herbivory in the canopy of black locust, *Robinia pseudoacacia*, after fertilization. Oikos 43:322–328

Hietz P, Turner BL, Wanek W et al (2011) Long-term change in the nitrogen cycle of tropical forests. Science 334:664–666. https://doi.org/10.1126/science.1211979

Hillebrand H, Dürselen C-D, Kirschtel D et al (1999) Biovolume calculation for pelagic and benthic microalgae. J Phycol 35:403–424. https://doi.org/10.1046/j.1529-8817.1999.3520403.x

Hillebrand H, Gruner DS, Borer ET et al (2007) Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. Proc Natl Acad Sci USA 104:10904–10909. https://doi.org/10.1073/pnas.0701918104

Holway DA, Case TJ (2000) Mechanisms of dispersed central-place foraging in polydomous colonies of the Argentine ant. Anim Behav 59:433–441. https://doi.org/10.1006/anbe.1999.1329

Kaspari M, Bujan J, Weiser MD et al (2017) Biogeochemistry drives diversity in the prokaryotes, fungi, and invertebrates of a Panama forest. Ecology 98:2019–2028. https://doi.org/10.1002/ecy.1895

Kay A, Zumbusch T, Heinen J (2010) Nutrition and interference competition have interactive effects on the behavior and performance of Argentine ants. Ecology 91:57–64

Klimes P, Idigel C, Rimandai M et al (2012) Why are there more arboreal ant species in primary than in secondary tropical forests? J Anim Ecol 81:1103–1112. https://doi.org/10.1111/j.1365-2656.2012.02002.x

Lanan MC, Dornhaus A, Bronstein JL (2011) The function of polydomy: the ant *Crematogaster torosa* preferentially forms new nests near food sources and fortifies outstations. Behav Ecol Sociobiol 65:959–968. https://doi.org/10.1007/s00265-010-1096-8

Longino JT (2007) A taxonomic review of the genus *Azteca* (Hymenoptera: Formicidae) in Costa Rica and a global revision of the aurita group. Zootaxa 1491:1–63. https://doi.org/10.1007/s10533-007-9087-1

Lubin Y, Montgomery G, Young O (1977) Food resources of anteaters (Edentata: Myrmecophagidae) I. A year's census of arboreal nests of ants and termites on Barro Colorado Island, Panama Canal Zone. Biotropica 9:26–34

Majer JD (1976) The maintenance of the Ant Mosaic in Ghana Cocoa farms. J Appl Ecol 13:123–144

Matsumura M, Trafelet-Smith G, Gratton C (2004) Does intraguild predation enhance predator performance? A stoichiometric perspective. Ecology 85:2601–2615

Mattson W (1980) Herbivory in relation to plant nitrogen content. Annu Rev Ecol Syst 11:119–161

Mooney KA, Halitschke R, Kessler A, Agrawal AA (2010) Evolutionary trade-offs in plants mediate the strength of trophic cascades. Science 327:1642–1644. https://doi.org/10.1126/science.1184814

Poelman EH, van Loon JJA, Dicke M (2008) Consequences of variation in plant defense for biodiversity at higher trophic levels. Trends Plant Sci 13:534–541. https://doi.org/10.1016/j.tplants.2008.08.003

Portha S, Deneubourg J, Detrain C (2002) Self-organized asymmetries in ant foraging: a functional response to food type and colony needs. Behav Ecol 13:776–781

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Room PM (1971) The relative distributions of ant species in Ghana's Cocoa farms. J Anim Ecol 40:735–751. https://doi.org/10.2307/3447

Sanders NJ, Crutsinger GM, Dunn RR et al (2007) An ant mosaic revisited: dominant ant species disassemble arboreal ant communities but co-occur randomly. Biotropica 39:422–427. https://doi.org/10.1111/j.1744-7429.2007.00263.x

Santiago LS, Wright SJ, Harms KE et al (2012) Tropical tree seedling growth responses to nitrogen, phosphorus and potassium addition. J Ecol 100:309–316. https://doi.org/10.1111/j.1365-2745.2011.01904.x

Schupp EW, Feener DH (1991) Phylogeny, lifeform, and habitat dependence of ant-defended plants in a Panamanian forest. In: Huxley CR, Cutler DF (eds) Ant-plant interactions. Oxford University Press, Oxford, pp 175–197

Sterner RW, Elser JJ (2002) Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton

Strauss S (1987) Direct and indirect effects of host-plant fertilization on an insect community. Ecology 6:1670–1678

Sun J, Liu D (2003) Geometric models for calculating cell biovolume and surface area for phytoplankton. J Plankton Res 25:1331–1346. https://doi.org/10.1093/plankt/fbg096

Thomas DL, Taylor EJ (1990) Study designs and tests for comparing resource use and availability. J Wildl Manage 54:322–330

Toft S, Wise DH (1999) Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different quality. Oecologia 119:198–207. https://doi.org/10.1007/s004420050776

Tschinkel WR (2015) The architecture of subterranean ant nests: beauty and mystery underfoot. J Bioecon 17(3):271–291

Vitousek PM (2004) Nutrient cycling and limitation: Hawai'i as a model system. Princeton University Press, Princeton

Vitousek PM, Sanford R (1986) Nutrient cycling in moist tropical forest. Annu Rev Ecol Syst 17:137–167

Vitousek PM, Porder S, Houlton BZ, Chadwick OA (2010) Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. Ecol Appl 20:5–15

Weber MG, Keeler KH (2013) The phylogenetic distribution of extrafloral nectaries in plants. Ann Bot 111:1251–1261. https://doi.org/10.1093/aob/mcs225

Wright SJ, Yavitt JB, Wurzburger N et al (2011) Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. Ecology 92:1616–1625

Wright SJ, Turner BL, Yavitt JB et al (2018) Plant responses to fertilization experiments in lowland, species-rich, tropical forests. Ecology. https://doi.org/10.1002/ecy.2193

Yanoviak SP (2015) Effects of lianas on canopy arthropod community structure. In: Schnitzer S et al (eds) Ecology of lianas. Wiley-Blackwell, New York, pp 345–361

Yavitt JB, Harms KE, Garcia MN et al (2009) Spatial heterogeneity of soil chemical properties in a lowland tropical moist forest, Panama. Aust J Soil Res 47:674–687. https://doi.org/10.1071/SR08258