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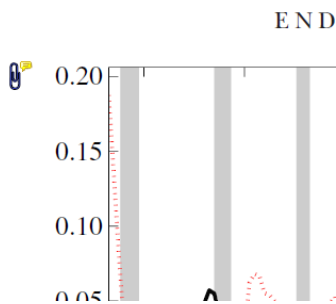
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Allows shapes, lines and freeform annotations to be drawn on proofs and for comment to be made on these marks.
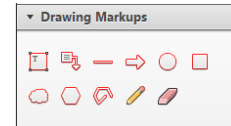
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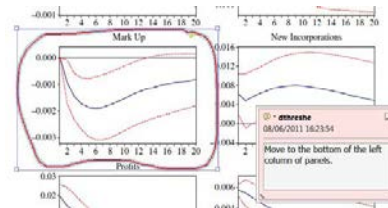
Biogeochemical drivers of Neotropical ant activity and diversity

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Abstract. Human activities are rapidly changing biogeochemistry across the globe, yet little is known about biogeochemical impacts on higher-level consumers. In a Panamanian rainforest, we measured the effects of chronic nitrogen, phosphorus, and potassium fertilization on ants: hyper-abundant terrestrial arthropods and ecosystem engineers. We tested two compatible hypotheses: the nutrient limitation hypothesis—where adding a limiting nutrient increases ant activity and abundance; and the community homogenization hypothesis—where adding a limiting nutrient decreases ant diversity. Lowland tropical rainforests are expected to be phosphorus-limited, so we predicted higher ant activity but lower diversity on phosphorus plots. In each fertilization plot, we baited trees and lianas to attract both canopy and ground nesting ants. After controlling for temperature, which accounted for roughly 20% of the variation in ant foraging activity, ant activity remained higher on phosphorus addition plots than on any other fertilization treatment. Genus level diversity was 16% lower on plots receiving phosphorus, than the control, consistent with the paradox of enrichment frequently observed in plant communities. This pattern, however, did not hold for species level diversity. The community-level response was largely driven by the most abundant genus, *Azteca* which increased foraging activity and abundance across phosphorus plots. The high activity and low diversity of ants on experimental phosphorus plots point to the potentially strong influence of biogeochemistry on these ubiquitous insects with potential ramifications for the forest food web. This is, to our knowledge, the first study relating biogeochemistry of macronutrients to foraging activity, diversity, and abundance of consumers, implicating strong bottom-up structuring of the ant community in one of the world's most diverse ecosystems.

Key words: *Azteca;* fertilization; Formicidae; Gigante; nutrient limitation; Panama; phosphorus; tropics.

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INTRODUCTION

Biogeochemistry imposes an elemental template on populations and ecosystems (Redfield 1958, Williams and Fraústo da Silva 1996, Sterner and Elser 2002), and the 25 elements required for life are not equally distributed across the globe. Fertilization experiments complement comparative studies (Richardson et al. 2004, Elser et al. 2007) to test for biogeochemical limitation of abundance, diversity, and function of organisms (Gruner and Taylor 2006, Hillebrand et al. 2007). In terrestrial ecosystems, most fertilization experiments have focused on primary producers (Tripler et al. 2006, Elser et al. 2007). Fertilization tends to reduce plant diversity (Hillebrand et al. 2007) while increasing plant biomass (Gruner et al. 2008) and plant nutrient content (Fox and Morrow 1992, Campo and Vazquez-Yanes 2004, Santiago et al. 2012). While nutrient limitation of plants may impact ecosystem's consumers (Oksanen et al. 1981, Power 1992, Mooney et al. 2010,

Schmitz 2010), few studies explore how forest fertilization affects the abundance of herbivores and predators (Forkner and Hunter 2000, Gruner and Taylor 2006) and these have done so using indirect measures, such as plant damage (Hargrove et al. 1984, Fox and Morrow 1992, Campo and Dirzo 2003, Santiago et al. 2012).

The geography of nutrient availability arises from the balance of deposition and weathering (Sterner and Elser 2002). In recently glaciated soils from high latitudes mineral phosphorus (P) is often relatively abundant through the deposition of glacial dust (Vitousek and Sanford 1986). In tropical forests, most biologically available P and potassium (K) must be weathered directly from bedrock; leaching decreases their supply over time (Walker and Syers 1976). Nitrogen (N) supplies, in contrast, tend to increase with time, through atmospheric deposition and biofixation (Vitousek 2004). Thus, forests growing on young soils are often N-limited (Vitousek and Howarth 1991), while forests growing on old weathered soils are often P-limited (Tanner et al. 1998, Wardle et al. 2004, Alvarez-Clare et al. 2013).

There is growing evidence for a major role of P limitation in tropical forests. Phosphorus fertilization can double plant growth rate in tropical montane forests (Tanner et al. 1990) and increase herbivore and predator abundance (Campo and Dirzo 2003, Gruner 2004). Evidence for P limitation of terrestrial consumers remains incomplete. Fertilization experiments rarely exceed 3 years, which can underestimate effects on long-lived organisms and slow processes (Tanner et al. 1990, Tilman and Wedin 1991). Moreover, of the three studies that exceed 3 years of fertilization in lowland tropical forests, none addressed responses of higher trophic levels (Mirmanto et al. 1999, Wright et al. 2011, Alvarez-Clare et al. 2013).

The Gigante fertilization experiment (GFP) consists of 32 40 × 40 m plots of lowland moist forest that have been fertilized with N, P, and K in a factorial block design for 16 years (Wright et al. 2011). The GFP offers a unique opportunity to explore how N, P, and K ramify through the forest's plants and limit the abundance, activity, and diversity of its consumers. Ants (Hymenoptera: Formicidae) are important consumers in most terrestrial ecosystems (Hölldobler and Wilson 1990). The ant populations of a tropical forest range from herbivores to specialized predators and scavengers, although the majority of ant species are omnivores, consuming plant, fungal, and animal tissue (Kaspari 2001, Blüthgen et al. 2003, Davidson 2005). Ant densities in the tropics can respond quickly (<1 month) to carbohydrate additions (Kaspari et al. 2012). Moreover, a colony's perennial and semi-sessile lifestyle (Keeler 1988, Gordon 1992) is suited to reflect long-term changes in biogeochemistry. Here, we test two consumer–resource hypotheses that predict the relationship between nutrient availability and food web structure.

Nutrient limitation assumes that at least one chemical element is at suboptimal levels such that increasing its availability enhances the survival and reproduction of a population. Long-term fertilization on the GFP increased N, P, and K concentrations in soil (Wright et al. 2011), seedlings (Santiago et al. 2012), and abscised leaves (Kaspari et al. 2008). Fertilization has also increased consumer activity reflected as the decomposition rate of cellulose on P and K plots (Kaspari et al. 2008), and understory herbivory on P, K, and PK plots (Santiago et al. 2012). This suggests that plants from P and K plots offer more palatable plant resources or that those plants are less defended (Coley et al. 1985). Moreover, these results suggest that P and K, but not N, are limiting in this forest. Thus, the positive effects of P and K fertilization on GFP herbivore and detritivore activity lead to the prediction that P and K plots should support higher ant activity (Blüthgen and Fiedler 2004) than N or control plots.

Community homogenization assumes that (1) species have different nutrient requirements and (2) increasing the supply of the limiting nutrient enables species that excel at resource uptake to outcompete species that can survive and reproduce at lower levels (i.e., have higher nutrient use efficiency). Resource availability and diversity often have a unimodal relationship, where the addition of a limiting nutrient increases diversity up to a threshold followed by a steady decrease in diversity (Tilman 1987, Sterner and Elser 2002). Over time, eutrophication reduces niche space and can ultimately lead to competitive exclusion by the species with the lowest resource use efficiency (Tilman 1987, Tilman and Wedin 1991, Harpole and Tilman 2007).

Community homogenization provides a mechanism for the paradox of enrichment (Rosenzweig 1971), where adding a limiting nutrient in excess reduces species richness (Sterner and Elser 2002). If tropical lowland forests are P-limited (Tanner et al. 1998), then P addition should favor the subset of species with high P uptake and low P use efficiency and thereby reduce diversity.

We know of no studies of how long-term changes in biogeochemistry, the building blocks of resources, have impacted ant communities. We build upon previous studies that examined how these experimental gradients of N, P, and K impact producers and herbivory, to test predictions about how long-term changes in biogeochemistry ramify through the food web to impact ant activity, abundance, and diversity. In doing so, we provide the first ecosystem level study exploring the consequences of long-term fertilization with multiple macronutrients (and their interactions) for a consumer community in a Neotropical forest as well as for an ant community in any biome.

Materials and Methods

We sampled ants during the rainy season in a lowland tropical forest on Gigante Peninsula within Barro Colorado Nature Monument (BCNM: 9°06′31″ N, 79°50′37″ W), Republic of Panama. Mean annual rainfall is c. 2600 mm and largely occurs during the rainy season from May–December, and mean annual temperature is 27°C (Leigh 1999). This old, secondary forest has been fertilized since 1998 with all factorial combinations of N, P, and K. Eight treatments (+N, +P, +K, +NP, +NK, +PK, +NPK, and control [CTR]) are replicated on four 40 × 40 m plots (Yavitt et al. 2009). Fertilizers are applied four times during the rainy season (for details, see Wright et al. 2011). Within each replicate, the +N, +P, +K, and +NPK treatments vs. the control, +NP, +NK, and +PK treatments form blocks to control for spatial variation in soils (Yavitt et al. 2009) and tree community composition (S. J. Wright, *unpublished data*) associated with a slight topographic gradient. This allowed us to further control for the potential effect of habitat heterogeneity on ant community composition.

To compare and quantify ant activity and species richness among fertilization treatments, we collected ants using bait transects. Baits are a standard sampling method for measuring ant activity (Bestelmeyer et al. 2000). We mixed two common baits—tuna and honey—to provide a bait that would (1) offer protein, lipids, carbohydrates, and salt; (2) be easily smeared on surfaces; and (3) could be made in quantity while maintaining consistent composition. In each fertilization plot, we set up two 30 m long and 1.6 m wide linear transects in cardinal directions crossing in the middle of the plot. Transects started and ended 5 m from plot edges. Along each transect, we baited every tree and liana stem at eye level, to attract both canopy and litter ants. At each fertilization treatment (four plots in total), the number of baits ranged from 239 to 304 depending on the density of understory vegetation, which was independent of the treatment received. We baited ants between 8:30 and 17:00 h in June and re-sampled the same plots in July of 2013. We sampled during the rainy season because ant activity in these forests is 25% higher compared to the dry season (Kaspari and Weiser 2000). Furthermore, at the beginning of the rainy season, most ants perform their mating flights (Kaspari et al. 2001), and colonies are expected to have higher nutrient requirements when taking care of the reproductive individuals. This is why we expected ants to be attracted by a rich resource provided as a bait more than they would be during a dry season. Sampling times were randomly assigned to the plots, the second time we sampled a plot we choose a different time of day, to minimize the temporal effects (e.g., if the plot was first sampled in the morning, re-sampling was made in the afternoon). We used the average of these two sampling events as a response variable in our activity analysis.

After 1 hour, we estimated the number of workers for each species on baits using a base 2 logarithmic scale (i.e., 1, 2, 4, 8, 16, 32, ...). We identified distinctive, common ants by eye (e.g., *Cephalotes atratus*, *Ectatomma ruidum*), and for all others, we collected workers into 95% ethanol for identification in the laboratory using an online database (evergreen.edu/ants/antsofcost arica.html), supplemented with a reference collection of the senior author. A subset of problematic identifications was further checked with barcode analysis (Basset, *unpublished data*). Voucher specimens are deposited in the laboratory of

the senior author and at the University of Panama. This allowed us to estimate activity and species richness of ants attracted to baits in each plot.

As ectotherms, ants are sensitive to changes in temperature; their activity is known to vary among species and increase at higher temperatures (Cerdá et al. 1998, Bestelmeyer 2000). Thus, we measured air temperature by aiming a portable IR thermometer (Fluke Corporation, Everett, Washington, USA; model 62) at eye level to a shaded spot >10 m away. We measured the temperature at the beginning and end of the two transects as soon as the baits were placed, and 1 hour later, when they were collected. In total, we took eight temperature readings per one baiting trial and used the plot mean temperature as a covariate in analyses.

We used a spherical densiometer to measure canopy openness at the center of each plot facing each cardinal direction. We used the mean of these four measurements in our analysis. Canopy cover was dense (85.8% ± 5.5%) and did not vary among fertilization treatments (Kruskal–Wallis: $\chi^2(7) = 4.4$, $P = 0.73$), so it is not included in our subsequent analyses.

Data analysis

We calculated foraging activity as the proportion of baits that were visited by ants. We used generalized linear mixed models (GLMMs) with binomial error distributions to evaluate relationships between ant activity, the factorial fertilization treatments (fixed effects), and temperature (a continuous covariate). The single random effect was comprised of spatial blocks. After accounting for slight overdispersion of our model using a random intercept which contains the same number of levels as our observations, we ran model selection based on an information theoretic approach. We dropped non-significant effects from the full model using probability values. We obtained P-values using the likelihood ratio tests of the full model against the model without the effect of interest (see Zuur et al. 2013 for details of model selection). After removing non-significant terms, we ran a model comparison based on ΔAIC values—the difference of the AIC of the ith model and the optimal model with the lowest AIC value. We repeated this analysis when testing the difference in ant activity of the

four most active genera. We tested the community homogenization hypothesis by examining the differences in Inverse Simpson diversity across nutrient additions and the differences in genus and species richness using GLMMs. Inverse of Simpson diversity index allowed us to examine diversity on a uniform scale (Hill 1973). We used a polynomial regression to test the effect of abundance of the most active genus across the plots—Azteca on ant richness and diversity. All statistical analyses were performed in RStudio (R Development Core Team 2012) using the "fossil" package (Vavrek 2011), "lme4" package (Bates et al. 2012), and "nlme" package (Pinheiro et al. 2012).

Results

Responses of ant activity to fertilization

Ant activity varied from 17% to 83% of baits occupied across our temperature range (Appendix S1: Fig. S1). Air temperature varied 4.5°C (24.3° to 28.8°C) over the course of our observations. Temperature accounted for almost one-fifth of the variation in foraging activity in both June ($y = 0.26x - 6.80$, $R^2 = 0.17$, $P < 0.001$) and July ($y = 0.22x - 6.22$, $R^2 = 0.19$, $P < 0.001$). Average activity increased 1.6-fold over this temperature range. As activity did not vary between June and July (paired t test, df = 31, $P = 0.26$), or across individual plots, we used the mean activity per plot across the 2 months.

Three GLMMs without any interaction terms, and without N as a fixed effect, had the lowest ΔAIC values and were used to analyze the effects of nutrient and temperature on ant activity (Appendix S1: Table S1). All together, these three models would be expected to be optimal models in 69% of cases (AIC Weights; Appendix S1: Table S1). Ant activity increased only on +P plots (i.e., +P, +NP, +PK, +NPK, $n = 16$, Fig. 1; Appendix S1: Table S1); average activity was 9% higher on +P plots compared to plots that did not receive P ($t = 2.1$, df = 25.4, $P = 0.04$).

The four most abundant genera were *Azteca*, *Dolichoderus*, *Ectatomma*, and *Crematogaster* which accounted for 86% of total ant activity. Only *Azteca* foraging activity increased across all +P plots, and the same three models as for overall activity are optimal in 53% of the cases (GLMM; Appendix S1: Table S2). Out of three added
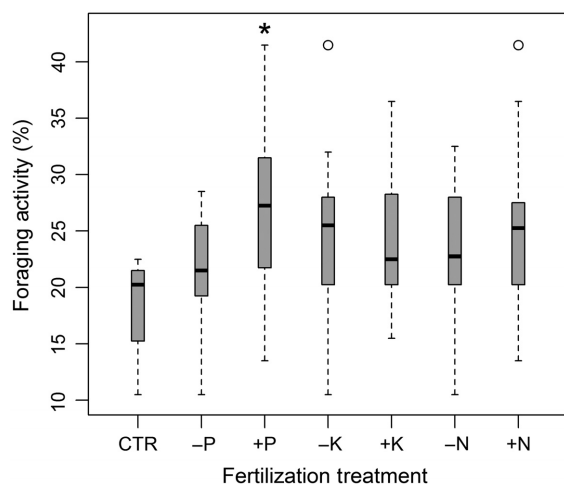
Fig. 1. Differences in foraging activity—number of baits visited by ants across: control plots—CTR; no phosphorus plots (−P): CTR, N, K, NK; phosphorus addition plots (+P): P, PK, NP, NPK; no potassium plots (−K): CTR, N, P, NP; all potassium plots: K, NK, PK, NPK; no nitrogen plots (−N): CTR, P, K, PK; all nitrogen plots: N, NK, NP, NPK. The box and whisker plots are showing median of foraging activity, upper and lower quartiles, as well as the maximum values and outliers.

nutrients, N was the worst, and P was the best predictor of *Azteca* activity, which was higher across +P plots by an average of 14% ($t = 2.2$, df = 28.0, $P = 0.04$). *Azteca* maximum activity was the highest on +P treatments, reaching up to 76% of all occupied baits on single P addition (Fig. 2A). *Dolichoderus*, the second most abundant genus, and in the same subfamily as *Azteca*, was not affected by +P, instead models including +N and +K treatments and their interactions best accounted for *Dolichoderus* activity in 41% of cases (GLMM; Appendix S1: Table S3). Phosphorus addition had no discernible effect on *Ectatomma*, *Crematogaster* (analysis not shown here).

Responses of diversity and richness to fertilization

We recorded a total of 82 ant species and 23 genera on the GFP (Appendix S1: Table S4), most of which were omnivorous ants (Appendix S1: Table S5). *Pheidole*, *Azteca*, *Camponotus*, and *Crematogaster* were the most species-rich genera, with 14, 9, 8, and 8 species. Given our activity data, we focused on single terms effects when testing for biogeochemical drivers of diversity.

Genus but not species diversity varied with fertilization treatment. Consistent with the paradox of enrichment, we found lower genus level diversity across +P plots compared to −P plots ($n = 16$; Inverse Simpson Diversity Index: mean ± SE: $D_P = 3.6 ± 0.4$, vs. $D_{noP} = 4.3 ± 0.3$). Models with +P and +K as predictors are optimal models in 45% of the cases, while models containing only +P are optimal in one-fourth of the cases (Appendix S1: Table S6). Across the seven treatments, genus diversity was highest on +N plots ($n = 4$; $5.3 ± 0.4$) and lowest on the NPK plots ($n = 4$; $3.1 ± 0.4$). In contrast, there was no difference in species diversity across +P plots compared −P ($n = 16$; $D_P = 5.0 ± 0.4$ vs. $D_{noP} = 5.5 ± 0.5$) or any other nutrient treatment, and the optimal models were indistinguishable from the model without any fixed effects (Appendix S1: Table S7).

Genus and species richness, the number of taxa observed, did not vary with fertilization. Genus richness trended lower on +P plots ($n = 16$; +P = $8.3 ± 0.3$ vs. −P = $9.3 ± 0.6$), but did not significantly vary across the fertilization treatments (Appendix S1: Table S8). Across the seven fertilization treatments, as with genus diversity, genus richness at was highest on +N ($9.8 ± 0.6$) and lowest on +NPK ($7.5 ± 0.5$). A similar pattern held for species richness where +N and control had the highest richness and +NPK the lowest (+N = $13.3 ± 1.0$; CTR = $13.3 ± 1.2$; vs. +NPK = $10.8 ± 1.1$; Appendix S1: Table S9).

As the activity of *Azteca* increased on +P plots, and genus level diversity decreased on +P plots, we examined the effect of the most active and most abundant genus on overall genus and species richness and diversity. While there was no relationship of mean *Azteca* abundance and diversity, we found a unimodal relationship of *Azteca* abundance and genus richness ($F_{2,5} = 17.2$, $P = 0.006$, $R^2 = 0.87$, Fig. 3). *Azteca* abundance, however, was not a good predictor of species richness ($F_{2,5} = 3.1$, $P = 0.14$, $R^2 = 0.55$, Fig. 3).

We quantified measures of richness using raw counts of genera and species as well as Simpson's inverse diversity, an index that increases with richness and evenness. Genus richness was a strong predictor of species richness ($y = 1.4x + 0.8$, $R^2 = 0.91$, $P < 0.001$; Appendix S1: Fig. S2),
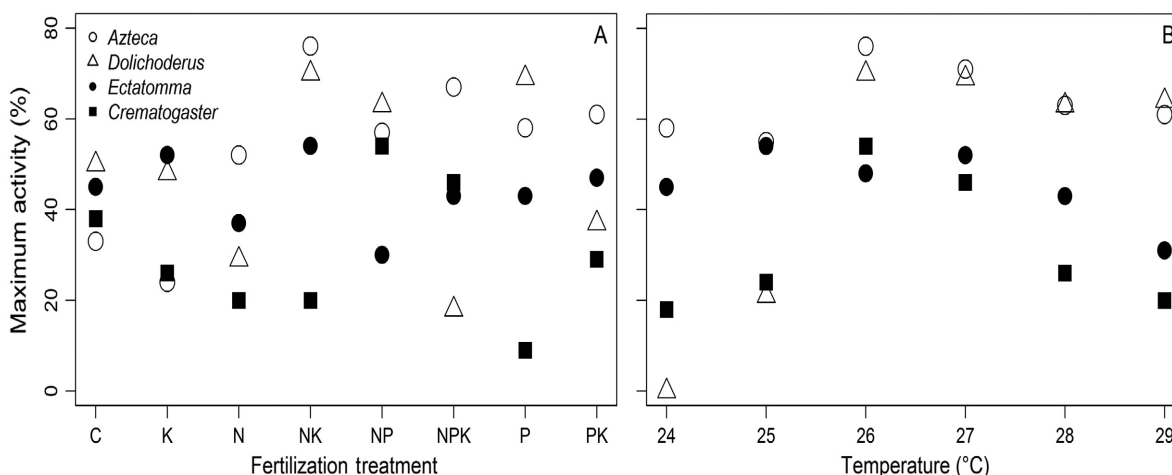
Fig. 2. Relationships between maximum activity (%)—maximum number of baits visited by ants across different fertilization treatments (A) and mean temperatures (B) for the most abundant genera at baits.

but accounted for less variability in the two measures that include evenness: genus diversity ($y = 0.4x + 0.4$, $R^2 = 0.78$, $P = 0.002$; Appendix S1: Fig. S3A) and still less in species diversity ($y = 0.3x + 2$, $R^2 = 0.50$, $P = 0.04$; Appendix S1: Fig. S3B). This is likely due to the frequency of genera (5, or 22%) and especially species (27, or 33%) that were recorded only once. Moreover,

almost half of the species singletons were found in only three genera (*Pheidole*—7% of the total species number, *Brachymyrmex*—5%, and *Camponotus*—4%).

Discussion

In a Panama forest, ant foraging intensity increased on plots after 16 years of P fertilization and genus diversity was lower on +P plots. *Azteca*, a numerically and behaviorally dominant ant genus (Davidson 2005), was implicated as a driver of these patterns. Three macronutrients (N, P, and K) have long been shown to promote plant productivity (Vitousek and Sanford 1986, Davidson 2004, Tripler et al. 2006) while lowering the plant diversity (Tilman and Wedin 1991, Hillebrand et al. 2007, Harpole and Suding 2011). Here, we show that increasing the availability of P, an element whose biogeochemistry is changing due to its increased use for agriculture (Cordell et al. 2009), has similar effects on a dominant set of consumers, the ants.

The effects of biogeochemistry and temperature on consumer activity

The increase in ant foraging activity on +P plots is mostly attributable to *Azteca*, as foraging of other ant genera did not increase with +P. Phosphorous availability may influence *Azteca* activity in a number of ways. Phosphorous fertilization, when combined with N and carbohydrate
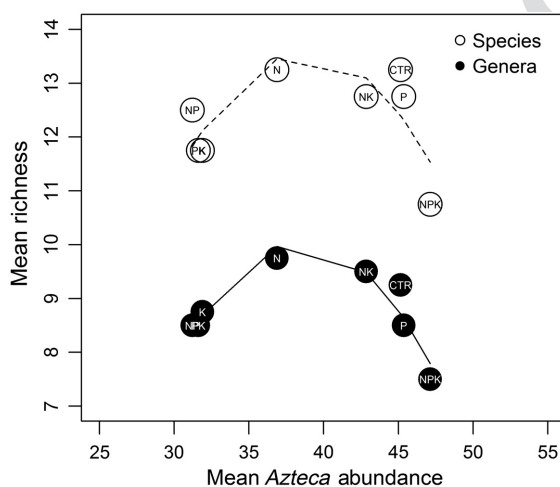

Fig. 3. The relationship between mean *Azteca* abundance at baits and species richness and genus richness. The relationship was significant for genus richness ($G = -0.06x^2 + 2.4x - 35.6$, $R^2 = 0.87$, $P = 0.005$) and not significant for species richness ($S = -0.02x^2 + 2.3x - 31.4$, $R^2 = 0.55$, $P = 0.14$).

addition, can increase the densities of potential prey such as gamasids, collembolans, and dermopterans (Jacquemin et al. 2012). Additionally, fertilization increased consumer activity since understory herbivory was higher on P, K, and PK plots of GFP (Santiago et al. 2012). This may alleviate the increased demand for protein during the wet season when most tropical ants rear their brood (Kaspari et al. 2001). Beyond increasing access to protein, P may also increase access to carbohydrates if P fertilization increases plant exudate secretion, or the abundance and activity of hemipterans that excrete honeydew (Schade et al. 2003, Perkins et al. 2004). Higher carbohydrate production can increase both foraging activity and aggression in ant colonies (Grover et al. 2007, Kay et al. 2010). For example, adding sucrose, but not protein, to litter plots in a nearby Panamanian rainforest increased the abundance of *Wasmannia auropunctata*, an aggressive litter ant, while reducing the abundance of other ant species (Kaspari et al. 2012). Specific group of herbivores and their impact across GFP have yet to be quantified; this would directly address the question of higher protein availability vs. higher honeydew availability. Finally, the increase in P concentration of plants on fertilized plots (Wright et al. 2011) may increase insect %P and %RNA (Schade et al. 2003). This could allow ants to increase their growth rate and colony size resulting in higher ant abundance and activity. To test this mechanism, P body content of ants from +P plots should be acquired, and our results suggest that focal species should be within the genus *Azteca*. We suggest these three mechanisms—an increased prey availability, higher availability of carbohydrate-rich food, and higher resource quality—act in concert to shape ant communities of tropical lowland rainforests.

Ectotherm activity is constrained by low temperatures (Huey and Kingsolver 1989). This appears to be true even in the narrow range of temperatures in tropical understories, where almost 20% of the observed variation in ant activity could be accounted for by an increase of just 4.5 degrees (24.3° to 28.8°C). This temperature range is typically associated with high ant activity in a variety of ecosystems (Cerdá et al. 1998, Bestelmeyer 2000, Retana and Cerdá 2000). Within this range, *Azteca* and *Dolichoderus* activity increased while *Ectatomma* and *Crematogaster*

activity decreased (Fig. 2B). Contrary to these findings, in a xerophyllus subtropical forest, *Ectatomma* and *Crematogaster* increased their activity within that same temperature range (Bestelmeyer 2000). These differences may be attributable to local adaptation (Angilletta et al. 2007) to the cooler temperatures of the moist Panamanian forest. However, we suggest that part of this decrease in activity by *Ectatomma* and *Crematogaster* is avoidance of the dominant *Azteca* and to a lesser extent *Dolichoderus*. *Azteca*'s large colony size, high colony density, chemical weaponry, and aggression allow them to exclude other ants from food resources (Davidson 2005, Dejean and Corbara 2007). Removing the large pendulous *Azteca* nests, and monitoring the responses of *Ectatomma* and *Crematogaster*, should allow us to evaluate these two hypotheses.

The effects of biogeochemistry and temperature on local diversity

We sampled ant activity and diversity on baits that simulate temporary resources. The diversity on baits should increase with the rate they are discovered and decrease with the rate that the subset of behavioral dominants—common in ant communities (Savolainen and Vepsäläinen 1988, Andersen 1992, 1997, Davidson 1998, Yanoviak and Kaspari 2000)—find and defend the baits.

Consistent with the paradox of enrichment (Rosenzweig 1971, Tilman 1987, Tilman and Pacala 1993), +P-fertilized plots tended to have fewer ant genera, compared to the plots which did not receive P addition. Moreover, genus richness showed a unimodal relationship with the average abundance of *Azteca* across plots (Fig. 3), linking +P plots to diversity via aggression by this behaviorally dominant genus (Andersen 1992). The mechanism for this effect may lie in the role P plays in limiting growth rates of animals and plants (Tanner et al. 1990, Elser et al. 2000). If dominance behavior by *Azteca* ants drives down diversity, the high-tempo and abundant workers of *Azteca* may be promoted on +P plots at the expense of smaller colonies of slower growing, more heavily armored ants (Davidson 2005). This pattern has been previously recorded at a long-term N fertilization experiment of a temperate grassland, where diversity of consumers decreased, but their abundance increased at higher N concentrations (Haddad et al. 2000).

Given that tropical forests differ considerably in nutrient availability (Vitousek 1984, Kaspari and Yanoviak 2009), we predict that forests rich in P should show higher levels of interference competition by ants and lower overall diversity than low P forests.

Caveats and next steps

Baiting is an efficient and easily repeatable method to estimate the abundance and activity of omnivores, which represent a large fraction of any ant fauna (Appendix S1: Table S5). Some ant species (e.g., fungus growers, specialist predators, and subdominant ants) are rarely attracted to the baits, or possibly displaced from them are likely undersampled in this study (Bestelmeyer et al. 2000). Other collection methods that do not rely on attracting ants, like litter sifting or pitfalls (Agosti and Alonso 2000), could supplement and further test these results to better represent the total diversity of ants in this Panamanian forest.

We found genus, but not species estimates of diversity and richness responded significantly to fertilization and the abundance of *Azteca*. One likely reason is that species data, with their larger fraction of singletons found in only three genera, are inherently noisier, and less conservative representations of community diversity and richness in the tropics given many genera remain poorly taxonomically resolved. Moreover, the higher number of singletons in species vs. genera and their concentration in only three genera are one likely reason that the variability in genus richness (CV = 22.2%) was lower than that for species diversity (CV = 32.2%). Given that genus and species richness data are often correlated, genus diversity in the Neotropical ants has been proposed as an efficient way of exploring biodiversity responses (Groc et al. 2010).

Conclusions

The industrial revolution has increased the availability of ecosystem C, N, and P (Mahowald et al. 2008, Cordell et al. 2009). Our data suggest the artificial enrichment of P may, through the paradox of enrichment, decrease ant diversity, and with it, the numerous ecosystem processes they provide (e.g., seed dispersal, scavenging, protection against herbivores, soil aeration, and nutrient turnover). What are the consequences of the increase in activity on +P plots—largely driven by *Azteca* compared to the variation due to diel temperature fluctuations? Understanding the mechanisms underlying P effects on *Azteca* activity, and its effects on other members of the ecosystem—plants and their secretions together with canopy and litter arthropods—will be instrumental when testing the mechanism behind the changes in consumer communities.

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