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Canopy Openness Enhances Diversity of Ant–Plant Interactions in the Brazilian Amazon Rain Forest

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ABSTRACT

In closed-canopy tropical forest understory, light availability is a significant determinant of habitat diversity because canopy structure is highly variable in most tropical forests. Consequently, variation in canopy cover affects the composition and distribution of plant species via creating variable light environments. Nevertheless, little is known about how variation in canopy openness structures patterns of plant–animal interactions. Because of the great diversity and dominance of ants in tropical environments, we used ant–plant interactions as a focal network to evaluate how variation in canopy cover influences patterns of plant–insect interactions in the Brazilian Amazon rain forest. We observed that small increases in canopy openness are associated with increased diversity of ant–plant interactions in our study area, and this change is independent of plant or ant species richness. Additionally, we found smaller niche overlap for both ants and plants associated with greater canopy openness. We hypothesize that enhanced light availability increases the breadth of ant foraging sources because variation in light availability gives rise to plant resources of different quality and amounts. Moreover, greater light availability promotes vegetative growth in plants, creating ant foraging 'bridges' between plants. In sum, our results highlight the importance of environmental heterogeneity as a determinant of ant–plant interaction diversity in tropical environments.

Abstract in Portuguese is available in the online version of this article.

Key words: abiotic factors; biodiversity; ecological interactions; interaction diversity; plant–animal interactions; tropical landscapes.

A CENTRAL GOAL OF ECOLOGY IS TO UNDERSTAND THE MECHANISMS THAT DETERMINE SPECIES COEXISTENCE in tropical ecosystems at different spatial and temporal scales (Stevens 1989, Wright 2002). Many factors have been proposed to explain the origin and maintenance of biodiversity in tropical environments (reviewed by Gaston 2000). One key factor shaping high species richness in the tropics is the great diversity of habitats, in which more heterogeneous landscapes (for beta diversity) and more variable microhabitats (for alpha diversity) can cause differences in habitat use by competitors and increase species coexistence (Dobzhansky 1950, Ricklefs 2004, Kennard *et al.* 2010, Zytynska *et al.* 2012). Thus, understanding the mechanisms that generate habitat diversity and how environmental heterogeneity affects biological communities are relevant to questions about the causes and consequences of biodiversity, and ultimately to issues surrounding the conservation of biodiversity (Tundisi *et al.* 1998).

Due to low incidence of solar radiation in the understory of closed-canopy tropical forests (Chazdon & Fetcher 1984, Oberbauer *et al.* 1988, Canham *et al.* 1990), light availability is an important resource and can be a factor that increases the diversity of habitats in these environments (Denslow & Hartshorn 1994, Gavin & Peart 1997). Variance in light levels affects the growth and survival of many plant species (Kellman & Tackaberry 1993) and allows shade-tolerant and light-adapted plant species to coexist, creating a mosaic of plant communities represented by different structures and successional stages (Denslow 1987, Montgomery 2004, Budke *et al.* 2008). These effects of spatial heterogeneity on the structure and spatial distribution of plants can also affect organisms that interact with them. Despite the well-documented effects of light availability on plant diversity, our current knowledge about the role of canopy openness structuring ecological interactions is limited to some studies on plant–herbivore interactions (Ribeiro & Basset 2007).

Ants (Hymenoptera: Formicidae) are a useful focal taxon for examining the influence of light availability on plant–animal interactions. In tropical rain forests, ants represent one of the most important organisms in terms of biological diversity and abundance (Fisher 1999, Longino *et al.* 2002). In these environments, it is very common to see ants foraging on plants, mainly due to the availability of food and nesting sites on and within plant tissues (Andersen 1990, Blüthgen *et al.* 2000, Davidson *et al.* 2003). Using an environmental biomarker approach, studies have shown that at a local scale ant and plant communities are extremely sensitive to microclimatic changes (Jones 1992, Brown 1997, Cerdá *et al.* 1997, 1998). However, these studies have examined ant and plant communities separately. It is equally interesting to document the effects of light availability and variance in other resources on interaction diversity (Thompson 1997)—in this case, the abundance and diversity of ant–plant interactions.

We hypothesized that if light availability directly influences plant growth, habitat complexity, and ant foraging (Nicotra *et al.* 1999, Reyes-Lopes *et al.* 2003), then variance in this abiotic factor will affect patterns of ant–plant interactions in closed-canopy forests. Specifically, we predict that an increase in light availability will

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indirectly cause decreased niche overlap due to greater resource availability (Hutchinson 1957) and an associated increase in diversity of ant–plant interactions. To test this hypothesis, we recorded the presence of ant–plant interactions in a closed-canopy tropical rain forest within the Brazilian Amazon and evaluated the effects of canopy openness on evenness and diversity of ant–plant interactions as well as niche overlap for ants and plants.

METHODS

Study area.—The fieldwork was carried out in a primary forest in the southern Brazilian Amazon, in the municipality of Cotriguaçu, north of Mato Grosso State. Specifically, we conducted the study on São Nicolau Farm (9°48′ S, 58°15′ W, 254 m asl; Vicente *et al.* 2012). The study site is located in an area of agricultural expansion referred to as the 'arc of deforestation' and the biodiversity of this threatened region is relatively unknown. The main vegetation within the 7000 ha of the forest consists of primary tropical rain forest, with canopy trees reaching 30–40 m in height and some emergent trees reaching 45 m. This closed-canopy forest has an understory that is relatively open with high densities of the understory plant, *Orbignya phalerata* Mart. (Arecaceae; Camargo *et al.* 2010). The terrain undulates, with approximately 40 m between plateaus and valleys. The climate, according to Köppen classification, is wet tropical (Am, Köppen classification) with an average annual temperature of 24°C, 85 percent humidity, and 2300 mm of precipitation. This Amazonian region presents two well-characterized seasons: a dry season (May to October) and a rainy season (November–April; Dáttilo *et al.* 2012).

Data collection.—We collected data in December 2010 and January 2011 at a study area managed by the Brazilian Research Program in Biodiversity (see http://ppbio.inpa.gov.br/). The sampling area consists of six parallel trails that are oriented north–south and two parallel trails that are east–west. Each stretch of 1 km on the trails was considered an independent sampling unit, consisting of 12 total sampling plots that were 250 m × 25 m (6250 m²; Dáttilo *et al.* 2013a; Fig. S1). All starting points of each plot were installed equally in one direction (east–west) along the same elevational isocline. At each of the 12 sampling plots, we collected all ants foraging on all plants that were accessible to the collector (from 0.5 m to 3 m high). We chose the first plant at the start of the sampling plot, and then we moved 10 m before choosing the next one, and then repeated this process. Therefore, we only used plants found at least 10 m apart to minimize the possibility of overestimating abundances of ant species with higher recruitment of workers and soldiers (*sensu* Gotelli *et al.* 2011). For each plant, we used a method similar to the 'entomological umbrella' (Bestelmeyer *et al.* 2000) in which all branches of a given plant were shaken and all the ants that fell were collected on a beat sheet placed under the branches. This method was very effective because some species, particularly of the genera *Camponotus* and *Ectatomma,* drop from the plant in response to the slightest disturbances (W. Dáttilo, pers. obs.). We used the entomological-umbrella method instead of feeding baits to minimize biases toward ant species with efficient recruitment behavior, with particular feeding habits, or that have an enhanced capacity to find baits. After collecting the ants via beating sample plants, we collected all ants and a plant sample for later identification. We excluded from our sampling any interactions between ants and myrmecophytes, as this kind of interaction can be extremely specialized and can require extensive natural history data to document (Bronstein 1998, Heil & McKey 2003).

To capture all the variance of light along the transects, in each sampling area we measured the canopy openness at six equidistant points (50 m) using a concave spherical densiometer. At each point we recorded four measurements (facing north, south, east, and west). The value representing the canopy cover of each sampling area was the mean of these four measures and subsequently, the mean of six points in each sampling area (Dáttilo *et al.* 2013a). Ants and plants were identified to the lowest possible taxonomic level by morphological comparisons with species deposited in collections from the Entomological Section of the Zoological Collection of the Universidade Federal de Mato Grosso, Brazil (CEMT), and the Herbário Centro–Norte Mato–Grossense (CNMT). Taxonomic specialists at these institutions also helped with identifications. Specimen vouchers were deposited in both the entomological collection and the herbarium of UFMT.

Data analysis.—Considering that plants can provide food resources to ants directly (*e.g.*, floral and extrafloral nectar and food bodies) and indirectly (*e.g.*, prey or honeydew of aphids), the ants' presence on such plants can indicate different categories of ecological interactions. In this study, we scored an ant species foraging on a plant species as an ant–plant interaction. This approach encompasses different types of ant–plant interactions, including: (1) mutualisms (protective ant–plant system); (2) neutral (ants using plants only as substrate); (3) antagonism (leaf-cutting ants); and (4) more complex indirect interactions that are both positive and negative. We examined the patterns of ant–plant interactions in 12 sampling areas using an ecological network approach. For this approach, we defined each sampling area as an adjacency matrix $\boldsymbol{A}$, in which A_{ij} represents the number of interactions between ant species i and plant species j in each sampling area (Bascompte *et al.* 2003). For each of the 12 networks of ant–plant interactions, we calculated the indices of interaction entropy (or interaction diversity: ID) and evenness of interaction distribution (IE), using the following formulas:

$$\mathrm{ID} = \sum p_a \log_2(p_a) \quad (1)$$

and

$$\mathrm{IE} = \frac{\sum p_a \log_2(p_a)}{\log_2 S} \quad (2)$$

where p_a is the proportion of the total number of ant–plant interactions (S) represented by interaction a. Both indices are based on the Shannon entropy and have been used widely for analyses of ecological networks (Bersier *et al.* 2002, Lewis *et al.* 2002, Sahli

& Conner 2006, Albrecht *et al.* 2007, Tylianakis *et al.* 2007, Blüthgen *et al.* 2008). These indices provide a quantitative measure of interactions that allows a direct comparison with previous work on interspecific interactions. We also calculated the niche overlap (NO) specifically for both trophic levels (ants and plants) using the Morisita–Horn index (Horn 1966):

$$\text{for ants: NO} = \frac{2\sum p_{ij}p_{ik}}{\sum p_{ij}^2 + p_{ik}^2}; \quad (3)$$

where, p_{ij} = corresponds to the proportion of plant species i used by ant species j; p_{ik} = corresponds to the proportion of plant species i of the total resource pool used by ant species k.

$$\text{for plants: NO} = \frac{2\sum p_{tl}p_{tk}}{\sum p_{tl}^2 + p_{tk}^2} \quad (4)$$

where, p_{tl} = corresponds to the proportion of ant species t shared by plant species l; p_{tk} = corresponds to the proportion of ant species t of the total resource pool used by plant species k.

This niche overlap index ranges from 0 to 1, where 0 indicates no common use of niches and 1 indicates complete overlap. Note that in this case i and j can be either plant or ant, and therefore, we have the niche overlap (or niche partitioning) for both ants and plants.

We used the Mao Tau moment-based rarefaction (Gotelli & Colwell 2001) to build rarefaction curves of ant and plant species recorded in our 12 sampling plots. In light of our large sampling effort, this technique can reduce the need for additional replicates (Colwell *et al.* 2004). In addition, we used the first-order Jackknife non-parametric species richness estimator for extrapolating species richness in the study area. Both analyses (rarefaction and richness estimation) utilized EstimateS 7.5.0 (Colwell 2005).

To test the hypothesis that the canopy openness affects the patterns of ant–plant interactions in our study area, we used general linear model regressions with canopy openness as a predictor variable for the following response variables: ant richness, plant richness, interaction diversity, interaction evenness, and niche overlap. We performed the regressions using the statistical programming language R v.2.1.3.1 (R Core Team 2012). Simple regressions were followed by path analysis to test for specific hypothesized causal relationships between canopy cover, interaction diversity, ant niche overlap, and plant niche overlap. We used SAS (SAS Institute Inc 2011) for this analysis. To assess the fit of the path model, we used the goodness of fit criterion ($P > 0.05$ indicates a good fit) and the Root Mean Square Error of Approximation (RMSEA—varies from 0 to 1, with values <0.05 indicating a good fit).

RESULTS

We recorded 1819 interactions involving 235 plant species (72 with extrafloral nectaries) and 149 ant species (Table S1). The family Fabaceae comprised 11.34 percent of plant species ($N = 27$ individuals), followed by 9.66 percent Bignoniaceae ($N = 23$), and 5.04 percent Moraceae ($N = 12$). Plant species richness per sampling area was 48.51 ± 3.42 (mean ± SE). For ants, the subfamily Myrmicinae comprised 35.57 percent of ant species ($N = 53$), followed by 29.53 percent for Formicinae ($N = 44$), and 17.44 percent for Dolichoderinae ($N = 26$). The ant species richness per sampling area was 31.12 ± 6.33. Although the species accumulation curves were characterized by a steep increase in the number of ant and plant species, no curve reached an asymptote. However, based on the estimates of asymptotes, we recorded 92.15 percent of plant species (235 species of 255 expected) and 90.85 percent (149 species of 164 expected) of ant species (Fig. 1).

Canopy openness did not affect ant or plant richness (Ants: $r^2 = 0.09$; $F_{1,10} = 1.050$; $P = 0.33$. Plants: $r^2 = 0.12$; $F_{1,10} = 1.472$; $P = 0.25$; Fig. 2A). However, we observed that small changes in canopy openness are significantly associated with patterns of ant–plant interactions in our study area. First, we found a high diversity of ant–plant interactions (mean ± SE: 4.75 ± 0.04) in all sampling areas. Moreover, diversity of interactions increases with greater canopy openness; diversity increased by 0.57 for one percent increase in canopy openness ($r^2 = 0.65$; $F_{1,10} = 10.120$; $P < 0.01$; Fig. 2B). We observed that the frequency of interactions was not dominated by individual species, as the interaction evenness was also high (0.98 ± 0.003), and this interaction metric was positively correlated with canopy openness; evenness increased by 0.04 for one percent increase in canopy openness ($r^2 = 0.78$; $F_{1,10} = 36.932$; $P < 0.01$; Fig. 2C). Finally, while the niche overlap of plants was higher than the niche

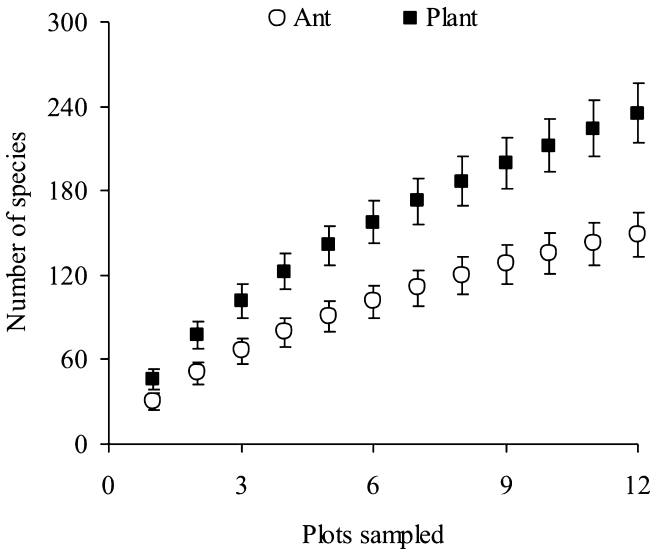

FIGURE 1. Species accumulation curves of ant and plant richness (Mao Tau) recorded in 12 sampling plots inserted in an undisturbed dense forest within the southern Brazilian Amazon, municipality of Cotriguaçu, north of Mato Grosso State between December 2010 and January 2011. The error bars represent the confidence interval of 95%.

overlap of ants, in both cases the values were particularly low (Ants: 0.11 ± 0.01. Plants: 0.23 ± 0.01). Moreover, sampling areas with higher canopy openness exhibit lower niche overlap for both trophic levels (Ants: $r^2 = 0.44$; $F_{1,10} = 9.438$; $P = 0.01$. Plants: $r^2 = 0.48$; $F_{1,10} = 7.977$; $P = 0.01$; Fig. 2D). Path analysis supported the causal hypothesis that light can lead to greater interaction diversity as well as restricted niche overlap for both ants and plants (the model was a significant fit to the data, $\chi^2 = 0.6$; df = 1; $P = 0.5$; RMSEA = 0; Fig. 3). When these direct relationships with light are statistically controlled in a causal path model, the data are consistent with this hypothesis: increased interaction diversity causes more restricted plant niche overlap, indirectly causing lower ant niche overlap via the positive effect of plant on ant niche overlap (Fig. 3).

DISCUSSION

A large number of studies have evaluated how different abiotic factors determine the composition and distribution of ants and plants at different scales in different ecosystems around the world (Sutherst & Maywald 2005, Ceccon *et al.* 2006, Menke & Holway 2006, Vasconcelos *et al.* 2008, Maestre *et al.* 2012). However, there are fewer studies that examine how ant–plant interactions are modified by variation in biotic and abiotic factors (Kersch & Fonseca 2005, Rico-Gray *et al.* 2012, Dáttilo *et al.* 2013b). The mechanisms that affect assemblages and diversity of ecological interactions also affect the structure and stability of species over space and time (Del-Claro & Torezan-Silingardi 2009, Dyer *et al.* 2010a, Tylianakis *et al.* 2010). While there are many factors that can affect ant communities, here we focused on one abiotic

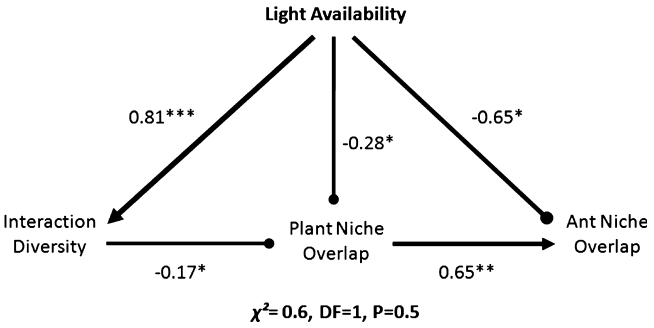

FIGURE 3. Path model testing direct and indirect causal effects of light availability (measured as canopy openness) on ant–plant interaction diversity, plant niche overlap, and ant niche overlap. Positive effects between variables are indicated by an arrow, negative effects are indicated by a bullet. Relationship strengths are indicated by the standardized path coefficient and thickness of arrow. Equations for interaction diversity and niche overlap are given in the text. High Type I error (*i.e.*, $P > 0.05$) for the χ^2 statistic indicates significant congruence between the data and the modeled causal relationships; based on the χ^2 statistic and an RMSEA estimate of 0, the model is a good fit to the data. The significance of the path coefficients is indicated as follows: *** < 0.0001, ** < 0.001, * < 0.01.

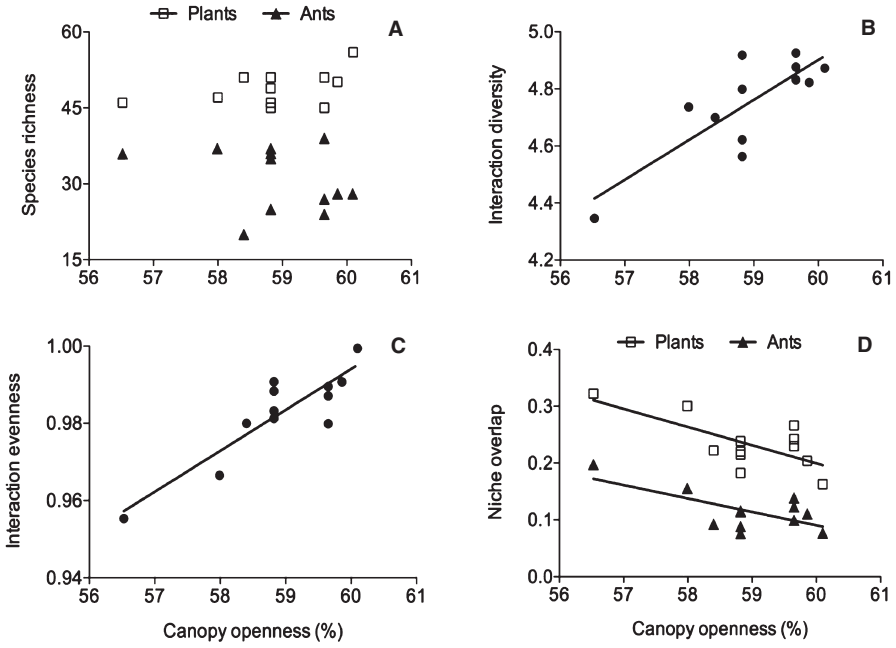

FIGURE 2. Results from general linear model regressions between canopy openness and: (A) ant and plant species richness (Ants: $r^2 = 0.09$; regression slope: 1.24; $P = 0.33$. Plants: $r^2 = 0.12$; regression slope: −1.97; $P = 0.25$); B) interaction diversity ($r^2 = 0.65$; regression slope: 0.14; $P < 0.01$; C) interaction evenness ($r^2 = 0.78$; regression slope: 0.01; $P < 0.01$); and D) niche overlap of ant and plant species (Ants: $r^2 = 0.44$; regression slope: −0.01; $P < 0.01$. Plants: $r^2 = 0.48$; regression slope: −0.03; $P < 0.01$). Data were collected in an undisturbed dense forest within the southern Brazilian Amazon, municipality of Cotriguaçu, north of Mato Grosso State between December 2010 and January 2011.

factor that affects diversity of ant–plant interactions in the Brazilian Amazon. We found that while canopy openness (light availability) did not influence ant and plant richness in our study plots, this factor directly increased diversity of ant–plant interactions by changes in evenness and decreased niche overlap for plants and ants. There are other factors that could also explain variance in ant–plant interactions, such as the plant species assemblages at different light levels, but we did have sufficient data to test for these indirect effects of light on interaction diversity.

Habitat heterogeneity is one important factor that has been proposed to explain differences in species richness on a local scale (*i.e.*, the habitat heterogeneity hypothesis, or just HHH, Williams 1943, Simpson 1949). The HHH predicts that the richness and diversity of species should increase in structurally complex environments (Tews *et al.* 2004, Cramer & Willig 2005). This is due to a greater diversity of habitat types and resource heterogeneity at these sites, which facilitates the coexistence of a greater number of species (MacArthur & MacArthur 1961, Pianka 1994). This hypothesis has been corroborated for both ants and plants in different ecosystems around the world (Bestelmeyer & Wien 2001, Ribas *et al.* 2003, Myklestad & Saetersdal 2004). However, using only variance in light availability as one indirect measure of environmental complexity, we observed that richness of plants and ants was not affected by light availability. This possibly occurred because environmental complexity in a given ecosystem is linked not only to the availability and distribution of a single resource such as light, but also by the arrangement of different biotic factors that can affect the richness and distribution of species (Lassau & Hochuli 2004, Tews *et al.* 2004). Another potential explanation, which is not mutually exclusive, is that there was insufficient variation in canopy cover in our study area to elicit a response in species richness at the sampling areas. Temperature is one of many factors associated with light availability and can alter niche partitioning and richness for ant communities (Mezger & Pfeiffer 2010, 2011). However, while the small changes in canopy cover (4%) could promote changes in the physiology of vegetation, these differences probably do not cause a significant increase in temperatures across a transect (Mezger & Pfeiffer 2010).

Light availability is a key factor regulating both nectar secretion and vegetative growth in plants (Shirley 1929, Szabo 1980, Kersch & Fonseca 2005). As our study area is a closed-canopy tropical forest, it is likely that small differences in canopy openness promote a significant increase in light availability in the understory. In turn, light availability is known to change some aspects of plant physiology, such as the amounts of nectar secretion or plant growth and resource allocation (Montgomery *et al.* 2003). Plants in habitats with higher light availability tend to secrete a higher quantity and better quality nectar (Radhika *et al.* 2010, Yamawo & Hada 2010) as well as increases in quality or quantity of other resources, such as food bodies (Dyer *et al.* 2004), which indirectly benefits trophic interactions between ants and plants (Kersch & Fonseca 2005, Burkle & Irwin 2010, Dyer *et al.* 2010b, Dáttilo *et al.* 2013a). At our study site, habitats with higher light availability were characterized by *Crematogaster*, *Brachymyrmex*, and *Ochetomyrmex*. Species of these three genera are frequently associated with plants bearing extrafloral nectaries (EFNs) (Del-Claro & Torezan-Silingardi 2009, Schoereder *et al.* 2010, Dáttilo *et al.* 2013a) with varying levels of overlap in utilizing this resource. In gaps at our sites we noted on several occasions intense recruitment of *Ochetomyrmex* (*O. semipolitus* and *O. neopolitus*) and *Brachymyrmex* ants to EFNs. The species of *Brachymyrmex* observed in field were not behaviorally or numerically dominant, and other species could be found tending EFNs nearby. In contrast, *Crematogaster* and *Ochetomyrmex* species were numerically dominant when associated with EFNs.

Another characteristic of plants growing in an environment with higher light availability is investment in faster vegetative growth and lower levels of antiherbivore defenses (Coley *et al.* 1985), often resulting in higher herbivory. We did not collect any leaf-cutter (*Atta* or *Acromyrmex*) species in our surveys, even in the habitats with higher light and potentially lower plant chemical defense. The absence of leaf-cutting ants was possibly a consequence of higher ant foraging for extrafloral nectar or for prey on foliage. Plant defense allocation strategies can cascade up to consumers, resulting in greater abundances of herbivores and higher resource availability for predators, including ants foraging on leaf surfaces (Dyer *et al.* 2004). Consequently, this also could increase the diversity of ant–plant interactions in environments with greater light availability. On the other hand, light availability can also increase the vegetative growth and number of connections between the leaves and branches, creating 'bridges' among plants, increasing ant foraging for different food resources (Andersen 2000, Powell *et al.* 2011). Thus, environments with greater light availability exhibit greater opportunities for ants to forage and to specialize on different food resources, resulting in a direct positive effect of enhanced light availability on the diversity of ant–plant interactions (Fig. 3).

We also found that higher canopy openness was directly and indirectly (via interaction diversity) associated with lower niche overlap for both trophic levels (Fig. 3). Ant species might differ in foraging strategies, and resource utilization by ants in more structurally complex environments is more segregated due to interspecific competitive interactions. Vegetation structure is one of the main mechanisms that promotes niche partitioning in ant communities, mainly because vegetative structural variation causes differences in microclimatic conditions, ant activity, availability of food, and nesting sites for ants (Retana & Cerdá 2000, Wang *et al.* 2001, Lassau & Hochuli 2004, Vasconcelos *et al.* 2008). Furthermore, our data supported the causal path analysis model that increased diversity of interactions under conditions of lower canopy cover caused decreased plant niche overlap, which in turn decreased ant niche overlap via a direct positive effect of plant on ant niche overlap (Fig. 3). This suggests that biotic interactions also contribute to strong niche partitioning and corroborates other empirical data that show that increased intensity or diversity of interactions is associated with higher levels of specialization and higher species diversity (Schemske *et al.* 2009, Dyer *et al.* 2010a).

Our results highlight the importance of environmental heterogeneity for determining patterns of ant–plant interactions in tropical forests. In sum, we found that the diversity and distribution of ant–plant interactions increased with increasing light availability, independent of species richness. However, it is important to consider that sites at the high or low ends of light availability could exhibit low heterogeneity of resources and habitats mainly due to the total absence or presence of light, which has a direct influence on the environmental heterogeneity at the local level (Monsi & Saeki 2005). Therefore, it is possible that sites with intermediate canopy cover may allow the coexistence of many species, specialized for different levels of resource availability. Finally, these results are relevant to conservation biology, mainly because environments with greater diversity of interactions tend to be more redundant in ecosystem functions and services (Kaiser-Bunbury *et al.* 2010, Pocock *et al.* 2012). For this reason, for future studies, we suggest that ecologists should quantify the resilience of environments with variable levels of interaction diversity in response to environmental perturbations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Map showing the spatial arrangement of the 12 sampling plots.

TABLE S1. *All ant–plant interactions recorded in the 12 sampling plots.*

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