

## Effects of an Epiphytic Orchid on Arboreal Ant Community Structure in Panama

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### ABSTRACT

Epiphytes are conspicuous structural elements of tropical forest canopies. Individual tree crowns in lowland forests may support more than 30 ant species, yet we know little about the effects of epiphytes on ant diversity. We examined the composition of arboreal ant communities on *Annona glabra* trees and their interactions with the epiphytic orchid *Caularthron bilamellatum* in Panama. We surveyed the ants on 73 trees (45 with *C. bilamellatum* and 28 lacking epiphytes) and recorded their nest sites and behavioral dominance at baits. We found a total of 49 ant species (in 20 genera), ranging 1–9 species per tree. Trees with *C. bilamellatum* had higher average ( $\pm$  SD) ant species richness ( $4.2 \pm 2.28$ ) than trees without epiphytes ( $2.7 \pm 1.21$ ). Hollow pseudobulbs (PBs) of *C. bilamellatum* were used as nest sites by 32 ant species, but only 43 percent of suitable PBs were occupied. Ant species richness increased with PB abundance in trees, but nest sites did not appear to be a limiting resource on *A. glabra*. We detected no close association between ants and the orchid. We conclude that higher ant species richness in the presence of the orchid is due to bottom-up effects, especially the year-round supply of extrafloral nectar. The structure of ant communities on *A. glabra* partly reflects interference competition among behaviorally dominant species and stochastic factors, as observed in other forests.

*Key words:* *Annona glabra*; *Caularthron bilamellatum*; myrmecophyte; tropical forest.

HABITAT STRUCTURE IS A FUNDAMENTAL DETERMINANT OF SPECIES RICHNESS in ecological communities (e.g., Dean & Connell 1987, Bell *et al.* 1991, Tews *et al.* 2004). The role of physical complexity in promoting the high arthropod diversity characteristic of tropical forest canopies (Erwin 1982, Stork *et al.* 1997) remains unclear. Epiphytes support diverse arthropod assemblages and are among the more conspicuous structural elements of the tropical canopy (e.g., Kitching *et al.* 1997; Ellwood *et al.* 2002; Stuntz *et al.* 2002; Yanoviak *et al.* 2003, 2004, 2006; Ellwood & Foster 2004). Here, we survey the arboreal ant fauna of tropical tree crowns with and without epiphytic orchids to test the hypothesis that epiphytes contribute to consumer diversity in this setting.

Ants represent a large fraction of animal biomass within tropical forest canopies (e.g., Fittkau & Klinge 1973, Tobin 1995, Davidson *et al.* 2003) and are embedded in a broad array of ecological processes (Hölldobler & Wilson 1990, Lach *et al.* 2010). Competition is one of the most important determinants of ant community structure, and in some arboreal settings, the effects of competition are apparent as a mosaic pattern of nonoverlapping species distributions (Rico-Gray & Oliveira 2007). Despite the effects of competition, and the physical constraints imposed by the structure of the canopy (e.g., Yanoviak & Kaspari 2000), a single tree embedded in primary tropical forest may support more than 30 ant species (e.g., Wilson 1987, Tobin 1995, Schulz & Wagner 2002). In most cases, the factors promoting coexistence of so many potential competitors are poorly known or not quantified (Rico-Gray & Oliveira 2007).

The evolutionary history of ants is closely associated with diversification of angiosperms (Moreau *et al.* 2006), and ecological links between ants and plants are common, especially in the tropics (Beattie 1985, Huxley & Cutler 1991, Rico-Gray & Oliveira 2007). Associations specifically between ants and epiphytes range from predation (*i.e.*, pruning) and opportunistic occupation, to apparent tight mutualism (Davidson & Epstein 1989, Yu 1994, Dejean *et al.* 1995, Ellwood *et al.* 2002, Stuntz *et al.* 2003, Céréghino *et al.* 2010). Despite the conspicuousness of these associations, the costs and benefits of ant occupancy to a host plant are often difficult to establish (Horvitz & Schemske 1984, Rico-Gray & Thien 1989).

Epiphytes generally provide two important resources for ants: physical niches (especially nest sites) and nutrients (nectar and hemipteran honeydew; e.g., Fisher *et al.* 1990, Fisher 1992, Catling 1997). Hollow plant parts are potentially limiting nest resources for arboreal ants, especially behaviorally subordinate taxa like *Campenotus* spp. and *Pseudomyrmex* spp. (Philpott & Foster 2005). In contrast, aggressive ants like *Azteca* spp. tend to build exposed carton nests (e.g., Adams 1994), and their occupancy of a tree often does not depend upon the availability of natural cavities. Plant-derived carbohydrates fuel the activities of *Azteca* and other behaviorally dominant arboreal taxa (Yanoviak & Kaspari 2000, Davidson *et al.* 2003, Rico-Gray & Oliveira 2007), and may control ant community structure via tritrophic interactions (Blüthgen *et al.* 2004). Consequently, epiphytes that provide both nest cavities and carbohydrates should increase local ant species richness by promoting the coexistence of behaviorally dominant and subordinate species.

Given the high species diversity of both trees and epiphytes in tropical forests (e.g., Croat 1978, Gentry & Dodson 1987, Benzing

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1995), isolating the effects of each on arboreal ant diversity is challenging due to the large number of potentially confounding factors. Here, we attempt to control for such differences by focusing on ant communities of a single tree species (*Annona glabra* L.; Annonaceae) and one of the most common epiphyte species that colonize it (*Caularthron bilamellatum* [Rch.f.] Schult.; Orchidaceae; see Zotz *et al.* 1999, Laube & Zotz 2007). Each *C. bilamellatum* plant produces multiple pseudobulbs (PBs), which develop a central cavity with age. Ants often nest within these cavities, typically entering through an opening at the PB base (Croat 1978, Fisher 1992, Dutra & Wetterer 2008). Ants also visit the extrafloral nectaries (EFNs) of *C. bilamellatum*, which occur on various parts of the plant (Fisher & Zimmerman 1988, Fisher *et al.* 1990).

We used this relatively simple system to test the hypothesis that epiphytes enhance ant diversity in tree crowns. Because the orchids provide nest and carbohydrate resources for arboreal ants, we expected higher ant species richness in the presence of the orchid and increased richness with increasing orchid density. Alternatively, if the effects of behavioral dominance overshadow resource limitation, richness differences are not expected to follow epiphyte distributions. To explore these potential mechanisms, we addressed the following questions: (1) What is the species composition of resident ant communities on *A. glabra* and how does composition change in the presence of *C. bilamellatum*? (2) What is the contribution of *C. bilamellatum* to available nest site densities for arboreal ants? (3) Do certain ant species consistently colonize *C. bilamellatum*? And (4) what are the effects of behaviorally dominant species on ant community structure in *A. glabra*? If ants use the orchid opportunistically (Fisher 1992), we expect similar species composition between trees with and without *C. bilamellatum*. Alternatively, consistent addition of one or more ant species in the presence of the orchid would suggest mutualism.

## METHODS

Field research was conducted at the Barro Colorado Nature Monument (BCNM) in the Panama Canal Zone (9°09'25" N, 79°50'40" W) between October 1998 and January 1999. The BCNM consists of Barro Colorado Island, several small islands, and three mainland peninsulas, all supporting semideciduous tropical lowland forest. Annual rainfall averages 2600 mm with a pronounced dry season from late December to April (see Croat 1978, Leigh *et al.* 1996 for additional details).

The focal tree species, *A. glabra* (Annonaceae), is common along shorelines in the BCNM. It is an evergreen, multi-stemmed tree, 3–8 m tall, and with rough bark. The trunk bases of most *A. glabra* were submerged during the study period, so we defined an individual tree as a group of stems with interconnected branches separated from other groups of stems by more than 1.5 m. Study trees existed on peninsulas comparable in exposure and tree density, had similar crown size, were 5–6 m tall, and consisted of 1–7 stems.

We observed and collected ants on 73 *A. glabra* trees in two categories: (1) completely free of epiphytes ( $N=28$ ) and (2) with *C. bilamellatum* as the only epiphyte present ( $N=45$ ). The ants on each tree were studied during daylight for at least 2 h following

placement of tuna baits on all branches and stems. We determined the location and number of nest sites by visually following ants departing from baits. Ant species occupying more than half of the baits at the end of observations were considered behaviorally dominant for a given tree (*e.g.*, Yanoviak & Kaspari 2000). Representative samples of all ants observed were collected and identified to species or morphospecies. Voucher specimens were deposited in the collections of the Smithsonian Tropical Research Institute, Panama.

We estimated total arboreal ant species richness in *A. glabra* using rarefaction techniques (EstimateS; Colwell 2009), and we assessed overlap in species composition among focal trees with the incidence-based Sørensen similarity index (Chao *et al.* 2005). We quantified positive or negative associations between ant species with Fisher's exact test following the method of Ludwig and Reynolds (1988). Only species occurring on three or more trees were included in the calculations. We used nonparametric analyses in cases where assumptions of parametric tests were violated. All means are reported  $\pm 1$  SD.

The clumped distribution of *C. bilamellatum* prevented accurate assignment of individual PBs to specific plants. Consequently, we used 'stand' to refer to a well-defined group of PBs (*cf.*, Sanford 1968). We counted the number of *C. bilamellatum* stands and the number of PBs per stand in each focal tree crown. We noted the condition and number of leaves per PB, and assigned each to a size class based on height: < 5 cm, 5–10 cm, 10–15 cm, and > 15 cm.

We additionally harvested 171 stands from 24 randomly selected *A. glabra* trees (4–12 stands from each tree) for examination in the laboratory. For each PB in these stands, we measured length, maximum width, physical condition (desiccated, damaged, etc.), quantity and dimensions of base openings, number of leaves, and dimensions of the internal cavity (if present). Dry, brown PBs were considered dead. All ants inhabiting harvested PBs were counted and sorted according to workers, queens, alates, and brood. A given PB was defined as colonized when brood or more than five conspecific ants were found in its cavity. We also noted the presence of carton, detritus (ant colony waste), and nonant arthropods.

## RESULTS

We collected a total of 49 ant species (Table 1). Eight of these were only found in harvested orchids; all others were collected from stems and branches of the 73 focal trees (Table 1). We found an average of 3.8 ( $\pm 2.0$ ) ant species per tree (range = 1–9). The most common species were *Odontomachus ruginodis* (52% of the trees), *Camponotus cf. auricomus* (27%), and *Pseudomyrmex gracilis* (26%). Approximately half (46%) of the collected species occurred on fewer than three trees. The average Sørensen similarity between trees was 0.18 ( $\pm 0.04$ ). Total ant richness on the focal trees was predicted to be 56–71 species based on Michaelis–Menten and incidence-based estimators, respectively (Fig. 1). Thus, our collection effort captured 70–88 percent of the arboreal ant assemblage on *A. glabra*.

Significantly more ant species were found on *A. glabra* trees with *C. bilamellatum* ( $4.2 \pm 2.28$ ) than on trees without the orchid ( $2.7 \pm 1.21$ ; Wilcoxon two sample test,  $P < 0.007$ ). Likewise,

TABLE 1. Distribution of ant species among nest sites on 73 *Annona glabra* trees. Values are the number of detected nests. Each orchid stand (Orchid) was regarded as a separate nest site Unkn, nest site not determined for species indicated by X.

Species	Wood				Unkn
	Orchid	Dead	Living	Carton	
<b>Dolichoderinae</b>					
<i>Azteca</i> sp. 4*				2	
<i>Azteca forelii</i>			2	4	
<i>Azteca cf. trigona</i> *	30	21	15	5	
<i>Azteca cf. velox</i> *	16	3	1		
<i>Dolichoderus bispinosus</i>					X
<i>Dolichoderus debilis</i>					X
<i>Dolichoderus diversus</i>	1	1			
<i>Dolichoderus laminatus</i> <sup>b</sup>	1				
<i>Dolichoderus lutosus</i> <sup>b</sup>	1				
<i>Tapinoma melanocephalum</i>					X
<b>Formicinae</b>					
<i>Brachymyrmex</i> sp. 1					X
<i>Camponotus atriceps</i>	4	1			
<i>Camponotus cf. auricomus</i>	2	6	1		
<i>Camponotus cf. linnaei</i>		1			
<i>Camponotus mucronatus</i>		1			
<i>Camponotus novogranadensis</i> <sup>b</sup>	1				
<i>Camponotus sexguttatus</i>	4	2			
<i>Paratrechina</i> sp. 1	3	4			
<i>Paratrechina</i> sp. 2*	10	6	4	1 <sup>a</sup>	
<i>Paratrechina</i> sp. 3	2				
<i>Paratrechina</i> sp. 4	8	11			
<i>Paratrechina</i> sp. 5					X
<b>Myrmicinae</b>					
<i>Cephalotes minutus</i>	1				
<i>Cephalotes umbraculatus</i> <sup>b</sup>	1				
<i>Crematogaster</i> sp. 2*	31	13	6		
<i>Crematogaster crinosa</i> *	23	19	7		
<i>Cyphomyrmex</i> sp. 1			1		
<i>Monomorium floricola</i> *	9	20	25		
<i>Pheidole</i> sp. 1		1			
<i>Pheidole punctatissima</i>	1	1			
<i>Pheidole cf. flavens</i>	1	2	2		
<i>Pyramica epinotalis</i>	1				
<i>Solenopsis zeteki</i> *	3	9	5		
<i>Solenopsis</i> sp. 1 <sup>b</sup>	3				
<i>Solenopsis</i> sp. 3 <sup>b</sup>	1				
<i>Wasmannia auropunctata</i> *	5	2	4		
<i>Wasmannia rochai</i>	3		1		
<i>Xenomyrmex panamanus</i> <sup>b</sup>	1				
<b>Ponerimorphs</b>					
<i>Ectatomma ruidum</i>		1			
<i>Odontomachus ruginodis</i>	20	12	8	19	
<i>Odontomachus bauri</i>	3	1	1	3	
<i>Pachycondyla harpax</i>	1				
<i>Pachycondyla villosa</i> <sup>b</sup>	1				

TABLE 1. Continued

Species	Wood			Carton	Unkn
	Orchid	Dead	Living		
<b>Ecitoninae</b>					
<i>Neivamyrmex</i> sp. 2					X
<b>Pseudomyrmecinae</b>					
	1	5			
<i>Pseudomyrmex gracilis</i> *	1	5			
<i>Pseudomyrmex simplex</i>		10			
<i>Pseudomyrmex tenuissimus</i>					X
<i>Pseudomyrmex</i> sp. 1		2	4		
<i>Pseudomyrmex</i> sp. 6*		1			
Sum	183	156	87	34	8

<sup>a</sup>Occupied an abandoned termite nest.

<sup>b</sup>Only found in destructively sampled orchids.

\*Dominated baits on at least one tree.

average Sørensen similarity was somewhat higher among trees with *C. bilamellatum* ( $0.22 \pm 0.04$ ) than trees without the orchid ( $0.19 \pm 0.06$ ;  $P = 0.017$ ). Ant species richness showed only a weak increasing trend with the number of orchid stands per tree (linear regression:  $F_{1,43} = 3.51$ ;  $R^2 = 0.08$ ,  $P = 0.07$ ; trees without epiphytes excluded), but richness increased significantly with both the total number of PBs in a tree ( $F_{1,43} = 14.97$ ;  $R^2 = 0.26$ ,  $P < 0.0004$ ) and the PB density (number per stand) in a tree ( $F_{1,43} = 12.58$ ;  $R^2 = 0.23$ ,  $P < 0.001$ ). The latter is a rough measure of the size and age of the stands in a tree. Only *Camponotus sexguttatus* showed an apparent preference for trees with the orchid, occurring on seven trees, all of which carried *C. bilamellatum*.

We located at least one nest for the majority (83%) of the ant species found on *A. glabra* (Table 1). Ants nested in cavities in living or dead wood, under bark, inside *C. bilamellatum* PBs, and in

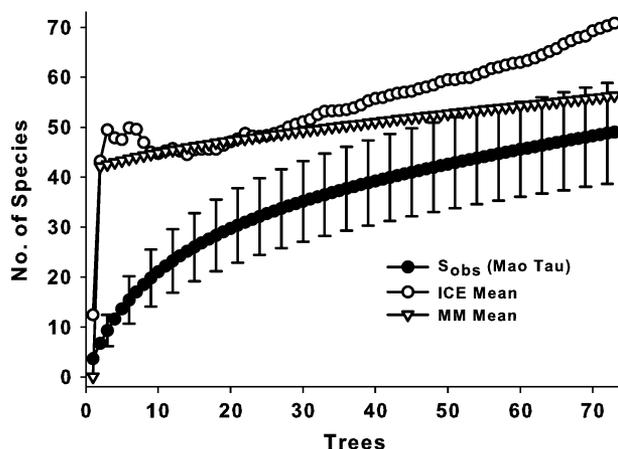


FIGURE 1. Ant species accumulation curves based on samples from 73 *Annona glabra* trees.  $S_{obs}$ , sample-based Mao Tau rarefaction curve ( $\pm 95\%$  CI; some bars omitted for clarity), MM, Michaelis–Menten richness estimator, ICE, Incidence-based coverage estimator. See Colwell (2009) for details.

self-constructed carton. Twelve species were found only in one nest type, but 11 of these had fewer than three nest records. Thus, nest preference results are only unequivocal for *Pseudomyrmex simplex*, which consistently nested in cavities in dead wood.

Eleven ant species exhibited behavioral dominance on at least one focal tree (Table 1). Single dominant species were found on most (71%) of the trees, 18 percent of trees had no dominant species, and the remaining trees were dominated by one of the following species pairs: *Crematogaster crinosa* and *Paratrechina* sp. 2, *C. crinosa* and *Solenopsis zeteki*, and *Monomorium floricola* and *Azteca* spp. Each species in a pair dominated a distinct set of stems, dividing a shared study tree into nonoverlapping territories. The number of subordinate species did not differ between trees with ( $2.3 \pm 1.53$ ) and without ( $2.4 \pm 1.78$ ) dominant ants (Wilcoxon test,  $P = 0.82$ ). However, average ant species richness was higher in trees with *Azteca* spp. ( $6.4 \pm 2.23$ ) than in trees lacking *Azteca* spp. ( $3.3 \pm 1.82$ ,  $P = 0.015$ ). Observations of nearby trees not included in our survey showed that individual colonies of behaviorally dominant species inhabited 8–25 neighboring trees of a shoreline sector, most of which were connected by lianas.

Analysis of 253 species pairs yielded ten positive and three negative associations (Table 2). *Odontomachus ruginodis* and *Odontomachus bauri* were negatively associated with each other (Table 2), but co-occurred with most other behaviorally dominant species. These two species occupied baits close to their nests during daytime, where they also preyed on other ant species. However, peak activity of both species was at night, when they dominated most baits on the entire tree (S. M. Berghoff, pers. obs.). Because we focused on the diurnal fauna of *A. glabra*, and given the temporal separation between *Odontomachus* spp. and other dominants, we did not classify the *Odontomachus* spp. as behaviorally dominant in this study.

We measured the characteristics of 542 *C. bilamellatum* stands (collectively including 3292 PBs). Trees with the orchid supported

an average of 10.3 stands ( $\pm 8.1$ ; range = 1–33), and individual stands had an average of 6.1 PBs ( $\pm 7.5$ ; range 1–68). The majority of stands (67%) had fewer than six PBs. Most (61%) of the living PBs had at least one leaf (max = eight leaves), and most (80%) had 1–3 openings at their base, which ranged from 0.5 to 26 mm in largest dimension.

In all, 32 ant species were found to nest at least occasionally in *C. bilamellatum* (Table 1). *Crematogaster* spp. and *Azteca* spp. were the most common inhabitants, respectively, occupying 30 and 25 percent of the stands that were found to contain an ant nest. However, dissection of stands revealed that most PBs (58%) were unsuitable for colonization by ants: 20 percent lacked an opening; 21 percent had an opening but lacked an internal cavity; and 17 percent possessed both an opening and cavity, but were significantly damaged (Fig. 2). The remaining PBs (42%) appeared suitable for colonization by ants, but only ca 43 percent of these contained ant nests. The size of a PB was not correlated with the number of ant workers (Spearman  $\rho = 0.131$ ,  $P = 0.09$ ) or brood present ( $\rho = 0.003$ ,  $P = 0.97$ ). Detritus and carton were found inside 12 percent of dissected PBs. In half of these, up to five roots had entered the cavity, growing appressed to the inner walls.

Scale insects (Hemiptera:Coccidae) occurred in 3 percent of the dissected PBs. Six of these lacked ants, while the other 23 were occupied by either *C. crinosa* or *Azteca* cf. *velox*. We found no relationship between the presence of ants and scale insects ( $\rho = 0.018$ ,  $P = 0.76$ ), but the three most common nonant arthropod taxa (Acarina, Collembola, and Diplopoda) were negatively associated with the presence of ants in PBs ( $\rho < 0.170$ ,  $P < 0.003$  in all cases).

TABLE 2. Associations between ant species pairs on *Annona glabra*.

		<i>P</i>
Positive associations		
<i>Pseudomyrmex</i> sp. 1	<i>Azteca</i> cf. <i>velox</i>	0.001
<i>Paratrechina</i> sp. 4	<i>Pheidole</i> cf. <i>flavens</i>	0.002
<i>Pseudomyrmex</i> <i>gracilis</i>	<i>Azteca</i> cf. <i>trigona</i>	0.004
<i>Pseudomyrmex</i> sp. 1	<i>Camponotus</i> cf. <i>auricomus</i>	0.004
<i>Paratrechina</i> sp. 4	<i>Azteca</i> cf. <i>trigona</i>	0.007
<i>Odontomachus</i> <i>ruginodis</i>	<i>Pseudomyrmex</i> <i>gracilis</i>	0.013
<i>Dolichoderus</i> <i>diversus</i>	<i>Camponotus</i> cf. <i>auricomus</i>	0.018
<i>Odontomachus</i> <i>bauri</i>	<i>Azteca</i> cf. <i>velox</i>	0.026
<i>Pseudomyrmex</i> <i>simplex</i>	<i>Solenopsis</i> <i>zeteki</i>	0.033
<i>Monomorium</i> <i>floricola</i>	<i>Azteca</i> cf. <i>trigona</i>	0.042
Negative associations		
<i>Odontomachus</i> <i>ruginodis</i>	<i>Odontomachus</i> <i>bauri</i>	0.023
<i>Crematogaster</i> <i>crinosa</i>	<i>Crematogaster</i> sp. 2	0.030
<i>Crematogaster</i> <i>crinosa</i>	<i>Azteca</i> cf. <i>trigona</i>	0.030

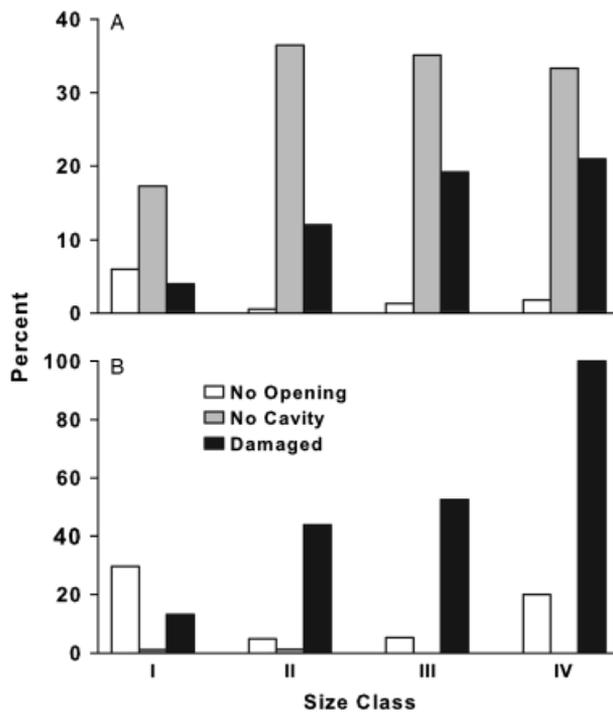


FIGURE 2. Size class distribution of living (A) and dead (B) pseudobulb characteristics relevant to their suitability as nesting site for ants. Class I = < 5 cm in height, Class II = 5–10 cm, Class III = 10–15 cm, Class IV = > 15 cm.

## DISCUSSION

Although animal diversity is often linked to structural complexity in vegetation (Pianka 1966), studies of vegetation structure and ant diversity have given mixed results (e.g., Ribas *et al.* 2003, Stuntz *et al.* 2003, Lassau & Hochuli 2004). Here, we show that *A. glabra* tree crowns occupied exclusively by the epiphytic orchid *C. bilamellatum* have 50 percent more arboreal ant species than trees without epiphytes. This increase was not due to the presence of specialized orchid inhabiting taxa. The eight species found only in dissected orchid stands are common in the BCNM forest canopy (S. P. Yanoviak pers. obs.). This suggests that occupancy of *C. bilamellatum* by ants is opportunistic and facultative, as observed in other studies of this system (Fisher & Zimmerman 1988, Fisher *et al.* 1990, Fisher 1992, Dutra & Wetterer 2008). Our expectation of higher species similarity in trees with the orchid than trees without the orchid also was supported; however, the difference in overlap between the groups was minimal (*ca* 3%) and arguably unimportant biologically.

We attribute higher ant species richness in the presence of the epiphytes primarily to bottom-up effects, specifically increased availability of EFN and physical structure for nest sites. Unlike most other epiphytes, *C. bilamellatum* provides EFN year round, and this resource is used by a variety of ant species (Fisher & Zimmerman 1988, Fisher 1992). In contrast, *A. glabra* does not produce EFN, and trophobionts (Davidson *et al.* 2003) appear to be relatively uncommon in this system. Variation in carbohydrate resources may have important ecological and behavioral consequences for arboreal ants (Rico-Gray & Oliveira 2007). Coccids and other trophobionts produce relatively high-quality honeydew and are often tended by a single aggressive species, whereas EFN attracts more ant species that forage together even in the presence of behaviorally dominant taxa (Blüthgen & Fiedler 2004, Blüthgen *et al.* 2004). Thus, a continuous supply of relatively low-quality EFN may promote ant species coexistence by influencing the behavior of dominant ants (*cf.*, Tillberg 2004). If so, experimental addition of trophobionts to the orchids or host trees should reverse this pattern.

Although we did not separate the independent contributions of nutrients and structure to ant diversity in this study, nest sites did not appear to be a limiting resource for ants on *A. glabra*. Most ant species occurred on trees both with and without *C. bilamellatum*, most were polydomous, and almost all occupied more than one type of nest (Table 1). Although the size range of the PB base openings could accommodate all observed ant species, unoccupied orchid stands were common in the focal trees, as were vacant wood cavities (S. M. Berghoff, pers. obs.). Clearly the orchids contribute to the physical complexity of the tree crowns and provide a diversity of physical niches for colonization by ants, but ant use of this additional structure is incomplete and opportunistic.

As in trees of agroecosystems (e.g., Catling 1997), the dominant ant species in *A. glabra* are distributed in mosaic-like patterns and predictably co-occur with certain subordinate species (Blüthgen & Stork 2007, Rico-Gray & Oliveira 2007). Ant mosaics are often established around a stable food source (Jackson 1984), and the EFN of *C. bilamellatum* may fill that role. However, sim-

ilarity in the number of subordinate species in trees with and without dominant species, and higher total richness in the presence of *Azteca* spp., suggest that stochastic factors also are relevant to ant species colonization and persistence in *A. glabra* (e.g., Floren & Linsenmair 2000). Differences between our results (e.g., ant species composition and occupancy rates) and other studies (e.g., Fisher & Zimmerman 1988, Fisher 1992, Dutra & Wetterer 2008) further suggest that stochastic factors are important in this system.

Average ant species richness in *A. glabra* (*ca* four species per tree) is considerably less than the richness often encountered in fogging-based surveys of lowland tropical tree crowns (e.g., Wilson 1987, Tobin 1995, Schulz & Wagner 2002). We attribute this to two factors. First, insecticide fogging captures a large number of stray (nonresident) species represented by few individuals (Floren & Linsenmair 2000). By contrast, baiting tends to undersample stray species, but has the advantage of unambiguously identifying key community characteristics, especially the composition of resident ants in each tree crown and the behavioral dominance status of each species (e.g., Yanoviak & Kaspari 2000, Tanaka *et al.* 2010). Second, *A. glabra* trees are relatively small, highly exposed, and often partially submerged. These characteristics likely exclude some forest interior species and semi-arboreal ground-nesting species (e.g., *Ectatomma* spp., *Paraponera clavata*, attines). Consequently, comparison of ants inhabiting *C. bilamellatum* of emergent trees in the forest interior with those of the shoreline would be an informative extension of this project.

We focused on the broad effects of the distribution of an epiphyte on ants. However, ants may also influence characteristics of epiphyte populations (e.g., Catling 1997). We do not know the colonization history of epiphytes on the focal trees, but the lack of ant gardens or close association between ant species and *C. bilamellatum* suggest that ants do not play a major role in determining their distribution. Apart from the negative association between ants and some nonherbivorous arthropods, we found no evidence that the ants influence the presence of other insects on the orchids, and only a small fraction of PBs suitable for colonization by ants contained detritus or carton.

In sum, our observations suggest that nutritional and structural resources provided by *C. bilamellatum* increase ant species richness in *A. glabra* crowns. Uncovering the specific mechanisms for this effect will require experimental manipulation of variables such as the age and density of orchids, the presence and composition of carbohydrate resources, or the distribution and abundance of behaviorally dominant ant species. Examination of ant activities at night also may further explain patterns of diversity, given the temporal shift in composition of the behaviorally dominant species observed in this study, and the increased frequency of EFN foraging at night (Fisher & Zimmerman 1988). Ultimately, identifying the contribution of epiphytes to ant diversity is an important step toward understanding of broader biodiversity patterns in tropical forests.

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