Temporal and trophic niche overlap in a guild of flower-visiting ants in a seasonal semi-arid tropical environment

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ABSTRACT

Studies of assemblages of insects that have largely agonistic relationships with plants are rare compared to those that study mutualistic relationships between plants and animals. Flowers have evolved multiple defense mechanisms to protect against nectar-thieving ants, which may decrease plant reproductive success. We evaluated season-specific patterns of biodiversity as well as trophic and temporal niche overlap for flower-visiting ants in the Brazilian Caatingas (dry scrub, tropical vegetation). Ant richness and evenness did not vary with season; however, Shannon diversity and Berger–Parker dominance were greater and lower, respectively, during the green season compared to the dry season. Trophic overlap was greater during the dry season than the green season. In contrast, temporal overlap was greater during the green season than the dry season. The most common flower-visiting ant (*Camponotus blandus*) exhibited season specific trophic and temporal niches. Flower-visiting ants exhibited seasonal complementarity, but within seasons species exhibited both trophic and temporal overlap, suggesting that competition for floral resources is not a strong structuring force in this guild.

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1. Introduction

Studies on flower visitor guilds that focus on agonistic interactions are scarce, as most studies evaluate mutualistic interactions between plants and animals (Vázquez et al., 2009). Insects receive nutritional resources in exchange for pollination (Blüthgen and Klein, 2011; Willmer et al., 2009) or protection (Mello et al., 2011; Santos et al., 2010). In addition, mutualistic interactions exhibit different levels of specialization (Aguiar and Santos, 2007; Santos et al., 2010), which affect the levels of redundancy or complementarity in the community (Blüthgen and Klein, 2011). Ecosystem functions are at increased risk when species are lost from communities with high rates of specialization and low levels of redundancy. Understanding redundancy in functions performed by species is important to inform conservation decisions and environmental policy within the context of pervasive negative anthropogenic effects on the environment.

Ants are common flower visitors, but their effects on plant fitness have not often been studied extensively. Flower-visiting ants can have positive or negative effects on seed production (Willmer et al., 2009) and thus could hinder or facilitate selection of flying pollinators, depending on ant abundance (Ashman and King, 2005). Ants and flying pollinators compete for nectar, and the presence of ants could alter aspects of plant reproductive success (increasing or decreasing it), such as self-pollination rate and male reproductive success (Ashman and King, 2005). In addition, the effect of flower-visiting ants on plant fitness may be dependent on aerial pollinator abundance, with positive effects of ants increasing as aerial pollinator abundances decrease (Holland et al., 2011). In general, mutualisms such as bee-plant and wasp-plant interactions have a high level of complementarity, which may manifest temporally, spatially, or as species-specific relationships (Blüthgen and Klein, 2011 and references therein). However, interactions of plants with flower-visiting ants can be detrimental to plant reproduction, as ants that harvest nectar from flowers generally are poor pollinators (Beattie et al., 1984; Junker et al., 2011). In addition, ants can damage the reproductive structures of flowers (Ashman and King, 2005; Galen, 1999) and negatively affect plant reproductive success.

As a response to nectar thieving by ants, plants have developed strategies to defend flowers against ants, such as extrafloral nectaries that lead ants away from reproductive structures, repellent substances, morphologies that prevent ant access to the nectar, mechanical barriers, and nectar that is unpalatable or toxic to ants (Holland et al., 2011; Junker et al., 2011; Willmer et al., 2009). Some of those barriers are always present (e.g., morphological adaptations); forcing ants to adapt morphologically or physiologically in

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order to overcome them (Junker et al., 2011; Willmer et al., 2009). In contrast, other barriers are present only occasionally (e.g., floral scents), as there are energetic and metabolic costs to produce chemical deterrents (Gershenzon, 1994). Effective occasional deterrents, such as scent production during anthesis, may cause ants to change their pattern of flower visitation (i.e., temporal activity; Junker et al., 2007; Willmer et al., 2009).

The pattern of flower visitation by ants may indicate which ant species can circumvent plant defenses, which ants can identify when flowers have available resources, or when plant defenses against theft are activated (Junker et al., 2007; Willmer et al., 2009). The selection mechanism should work in a way that allows ant species to identify resource availability and temporal gaps in plant defenses. A high degree of overlap (i.e., redundancy) in trophic niches or in temporal patterns of resource use among ants suggests that plants are generally unable to protect floral nectar (trophic overlap) or have temporal variation in the effectiveness of defenses (temporal overlap). Alternatively, if the flowers of some plant species are visited by only one or a few ant species, with different ant species visiting different plant species, multiple explanations are possible. In general, restrictions associated with guild membership or with physiological limitations seem to determine temporal activity patterns of animals, with little evidence of temporal niche segregation due to interspecific interactions (Castro-Arellano and Lacher Jr., 2009; Santos and Presley, 2010).

The Caatinga (seasonal semi-deciduous dry forest) is one of the least studied tropical biomes (Leal et al., 2008; Lewinsohn and Prado, 2002; Rodal et al., 2005). Caatingas have their geographic distribution determined by critical rainfall thresholds, and are highly seasonal, with a warm and dry season and a rainy season, also known as the green season (Leal et al., 2008; Rodal et al., 2005). This seasonality results in deciduous vegetation and drastic seasonal changes in resource productivity and availability, which are abundant in the green season and scarce in the dry season (Barbosa and Baethgen, 2006; Santos, 2006). In a recent review on insect seasonality in the Caatinga, Vasconcellos et al. (2010) showed a seasonal increase in insect activity and richness associated with rainfall. In dry tropical systems, habitat heterogeneity, resource availability, and abiotic factors (e.g., temperature, humidity) are important factors that affect ant species richness and composition (Neves et al., 2010). Ant diversity may increase during the rainy season, when more resources are available (Lindsey and Skinner, 2001); however, in some habitats responses may manifest as changes in species composition rather than species richness, with changes in composition dependant on the successional stage of the habitat (Neves et al., 2010).

Three main factors affect the temporal patterns of ants foraging on flowers in tropical dry regions: 1) times of the day or seasons of the year when very high temperatures cause physiological stress, thus foraging activities are restricted to less stressful times; 2) fluctuations in food availability during the day or throughout seasons, because plants make available nectar only at particular times or seasons (Gottlieb et al., 2005; Stone et al., 1999); and 3) ant response to occasional barriers imposed by plants to avoid resource theft at particular times or seasons (antagonistic interactions) (Bleil et al., 2011; Holland et al., 2011; Junker et al., 2011, 2007; Willmer et al., 2009).

There is no information on the use of floral resources by ants in the Caatingas or on the effect of seasonal vegetation dynamics on the composition and structure of the guild of flower-visiting ants. Niche overlap affects community structure, diversity, and ecosystem functioning, making niche-based research a useful platform for understanding the relationships between community structure and ecosystem function (Chase, 2011; Chase and Leibold, 2003). To evaluate the overlap of trophic and temporal niches of

flower-visiting ants, we collected data on flower visitation by ants in the Brazilian Caatinga, a biome with high seasonal variation in vegetation structure and a diverse flower-visiting ant assemblage. Productivity in the Caatinga changes greatly between the dry and the green seasons, which may affect the trophic or temporal niches of flower-visiting insects. Hence, we evaluated aspects of niche overlap separately for each season. We do not have sufficient data to powerfully test particular mechanisms associated with ant–plant interactions that may mold temporal or trophic niches of flower-visiting ants in the Caatinga; however, we can establish which patterns of temporal or trophic niche overlap are consistent with particular types of mechanisms. For example, if primary plant defenses to nectar theft by ants are temporally variable (e.g., floral scents only produced at certain times), temporal activity patterns of ant species should be more similar than expected by chance as all ants would exploit the resource when defenses were absent and avoid it when defenses were present. Depending on the scale of temporal variability in the plant defense mechanisms, responses may manifest in diel activity or as season-specific patterns. With respect to trophic niches, significant overlap is consistent with plant species lacking defenses against nectar theft, allowing all ant species to exploit nectar resources; niche segregation is consistent with specialization, in which plants and ants may have mutualistic relationships that allow only select species to use nectar. This suite of analyses should support some hypotheses regarding interactions between plants and flower-visiting ants, and help to focus future studies on hypotheses with the greatest amount of empirical support.

2. Material and methods

2.1. Study area

The present study was carried out in two areas of deciduous scrub vegetation in Milagres municipality, State of Bahia, northeastern Brazil (12°54′15″ S, 39°51′57″ W, elev. 480 m), located in the Caatingas morpho-climatic domain, which exhibits a tropical semi-arid climate. Detailed characteristics of the study area can be found in Bahia (1994) and França et al. (1997). The region exhibits strong seasonality, with long dry seasons characterized by droughts that last at least five months each year (Bahia, 1994), and a green and rainy season (usually from December to February), when there are vegetation blooms, including massive flowering events. The mean annual temperature is 23.1 °C, the maximum annual temperature is 28 °C, and the minimum annual temperature is 19.1 °C. The mean annual rainfall is 460 mm, ranging from 137 mm to 1035 mm.

2.2. Sampling

In order to test the effect of seasonal vegetation dynamics of the Caatinga on trophic and temporal aspects of ant niches, data were collected during each of two seasons (dry and green). During each session, two collectors carefully and simultaneously inspected each flowering plant for flower-visiting ants along a 350 m long and 10 m wide transect. Each transect was sampled for 11 consecutive hours (from 07:00 to 18:00), we carried out four sampling sessions during the dry season (on July 9–10, on September 5–6, 2009) and four sampling sessions during the green season (on December 11–12, 2009, on February 6–7, 2010) for a total of 176 collector-sampling-hours. Ants were collected only from the surfaces of flowers and only after they were observed to forage on nectar. The identity of flowering plant species were recorded only for plants that were visited by ants (i.e., a complete vegetative survey of transects was not performed). To avoid under- and oversampling,

each flowering plant was inspected for exactly 5 min, regardless the number of flowers per plants (method adapted from Sakagami et al., 1967). Vouchers were deposited in the Prof. Johann Becker Entomological Collection of the Zoology Museum of Universidade Estadual de Feira de Santana (MZFS) and in the herbarium of the same institution (HUEFS).

2.3. Data analysis

We estimated four aspects of biodiversity, species richness, Shannon diversity, Camargo's evenness (Camargo, 1993), and Berger–Parker dominance (Berger and Parker, 1970), for flower-visiting ants for each season. We used a null model approach to evaluate the statistical significance of seasonal differences for each diversity metric (Solow, 1993). For each analysis, individuals from both seasons were combined into a single pool of individuals. For each of 10,000 iterations, individuals from the combined pool were randomly assigned to two samples, with sample sizes constrained to equal the empirical sample sizes for the dry and green seasons. Diversity metrics were calculated for each pair of simulated samples and the differences between pairs of values was calculated. The 10,000 differences for each diversity metric formed the null distribution to which the empirical difference in diversity was compared to determine significance. Null model analyses were conducted as two-tailed tests with function "diversitydiff" written in MATLAB 7.8.0. MATLAB functions available for download from http://www.tarleton.edu/Faculty/higgins/Higgins.zip.

Trophic and temporal niche overlap between pairs of ant species was calculated with Schoener's index (1982). Trophic and temporal niches of species with small sample sizes may be poorly characterized. To avoid biases associated with poorly defined niche axes, we excluded all species with fewer than 5 observations for each season from analysis. A Kolmogorov–Smirnov 2-sample test was used to test for differences between each possible pair of species in dietary niche overlap as well as in temporal activity pattern (Siegel, 1956).

We evaluated assemblage-wide niche overlap for flower-visiting ants following the analytical methods of Gotelli and Entsminger (2001) for dietary niche overlap and of Castro-Arellano et al. (2010) for temporal overlap. Monte Carlo simulations were used to generate null distributions of overlap values among the common species (i.e., species with at least 5 observations during a season) of flower-visiting ants separately for each season. The basis of each analysis was an ant species by flower species or an ant species by time interval matrix of the relative number of captures recorded for each ant species on each species of flower or during each time interval. Overlap was quantified as the average of all pair-wise overlap values calculated via the Pianka (Pianka, 1973) and Czechanowski (Feinsinger et al., 1981) indices. To evaluate dietary overlap, we used randomization algorithm 3 (RA3; Winemiller and Pianka, 1990), which retains the niche breadth of each species of ant and randomly reshuffles the values for each trophic category for each ant species. This null model has a desirable combination of type I and type II error rates for evaluation of nominal data. For temporal activity, null distributions of overlap values were generated using a randomization algorithm (Rosario) that was designed specifically for use with interval data, in which the order of categories is important (Castro-Arellano et al., 2010). Rosario maintains the shape of the empirical activity distributions (i.e., temporal autocorrelation) for each species in the randomly generated matrices by shifting entire activity patterns a random number of intervals. For each analysis, overlap indices were calculated for 10,000 randomly generated matrices of dietary niche or of temporal activity patterns, creating a null distribution of overlap values. Significance was determined by comparing each

empirical value to its associated null distribution. Analyses of niche overlap were conducted as two-tailed tests. Coincidence in diet or temporal activity was indicated by significantly more overlap (i.e., $p \leq \alpha/2$) than expected by chance. Segregation in diet or temporal activity was indicated by significantly less overlap (i.e., $p \leq \alpha/2$) than expected by chance. Simulations for dietary overlap were conducted in EcoSim 7.72 (Gotelli and Entsminger, 2001); simulations for overlap in temporal activity were conducted with the TimeOverlap program (Castro-Arellano et al., 2010; program available for download at http://hydrodictyon.eeb.uconn.edu/people/willig/Research/activity%20pattern.html). For all analyses, we used an α of 0.05.

3. Results

We collected 34 ant species associated with flowers of 42 plant species. Camponotus blandus (Smith, 1858) (50.8%) and Cephalotes pusillus (Klung, 1824) (14.8%) were the most frequently observed ant species. Senegalia langsdorffii (Benth.), Ipomoea pintoi O'Donnel, Stigmaphyllon ariculatum (Cav) A. Juss., and Tacinga palmadora (Britton and Rose) were the plants most visited by ants.

During the dry season 117 individuals representing 23 ant species were observed visiting 22 plant species and during the green season 187 individuals representing 23 ant species were observed visiting 33 plant species. Only 12 ant species were observed during both seasons (35.3%), 11 ant species (32.35%) visited flowers exclusively during the dry season, and 11 ant species (32.35%) visited flowers exclusively during the green season. Ants visited 13 species of flowering plants during both seasons, 9 species only during the dry season and 20 species only during the green season (Table 1, Appendix A). Of the 34 ant species, only 10 were observed visiting flowers more then five times during the study.

Despite the fact that flower-visiting ant species richness did not differ between seasons (Table 1), some aspects of ant biodiversity were significantly different between seasons. Ants exhibited significantly greater Shannon diversity ($p = 0.034$) and significantly lower Berger–Parker dominance ($p < 0.001$) during the green season than during the dry season. In contrast, species richness ($p = 0.216$) and Camargo evenness ($p = 0.237$) did not differ significantly between seasons. Significant differences in biodiversity primarily are attributable to the increased dominance of C. blandus during the green season compared to the dry season.

3.1. Trophic niche overlap

Among species with ≥ 5 observations during a season, dietary overlap (Schoener's index) varied from 0.33 to 0.80 during the dry season, and varied from 0.06 to 0.80 during the green season (Table 2). The two most abundant ant species (C. blandus and C. pusillus) exhibited greater overlap during the dry season (0.63) than during the green season (0.44). None of the pair-wise comparisons exhibited significantly different trophic niche distributions during the dry season (Table 2) or during the wet season (Table 2). Average overlap in trophic niches was greater during the dry season (0.52) than during the green season (0.34). Of the four species that were recorded at least 5 times each season, only C. blandus exhibited seasonal differences in trophic niche (Kolmogorov–Smirnov 2-sample test, $p = 0.003$; Fig. 1A).

Dietary overlap for the common flower-visiting ant assemblage was significantly greater than expected by chance for the dry season (Pianka = 0.735, $p < 0.0001$; Czechanowski = 0.517, $p < 0.0001$) and for the green season (Pianka = 0.477, $p < 0.0001$; Czechanowski = 0.341, $p < 0.0001$). Flowers of S. langsdorffii, Stigmaphyllon auriculatum, I. pintoi and T. palmadora were the most visited by ants, representing 45% of all visits. Flowers of I. pintoi, T.

Table 1
Flower-visiting ants and four measures of ant biodiversity recorded for each season from the Brazilian Tropical dry forest.

Ants species	Code	Season	
		Dry	Green
Myrmicinae			
Acromyrmex sp1	Acr		X
Atta rubripilosa (Forel, 1908)	Att		X
Cephalotes clypeatus (Fabricius, 1804)	Cec	X	X
Cephalotes depressus (Klung, 1824)	Ced	X	X
Cephalotes minutus (Fabricius, 1804)	Cem		X
Cephalotes pilosus (Emery, 1896)	Cep	X	
Cephalotes pusillus (Klung, 1824)	Cpu	X	X
Crematogaster sp1	Cre	X	
Crematogaster sp2	Cr2	X	X
Pheidole sp1	Phe	X	
Pheidole sp2	Ph2	X	
Pheidole sp3	Ph3		X
Solenopsis sp1	Sol	X	
Dolichoderinae			
Azteca sp1	Azt	X	
Linepthema sp1	Lin	X	
Formicinae			
Brachymyrmex sp1	Bra	X	
Camponotus blandus (Smith, F., 1858)	Cbl	X	X
Camponotus sp2	Ca2	X	X
Camponotus sp3	Ca3	X	
Camponotus sp7	Ca7		X
Camponotus sp8	Ca8		X
Camponotus sp9	Ca9		X
Camponotus sp12	C12		X
Paratrechina sp1	Par	X	
Ectatomminae			
Ectatomma muticum (Mayr, 1870)	Ect		X
Gnamptogenys sp1	Gna		X
Pseudomyrmecinae			
Pseudomyrmex schuppi (Forel, 1901)	Pss	X	X
Pseudomyrmex sp1 gp *pallidus*	Ppa	X	X
Pseudomyrmex sp2 gp *pallidus*	Pp2	X	X
Pseudomyrmex sp3	Ps3	X	X
Pseudomyrmex sp4	Ps4	X	
Pseudomyrmex sp5	Ps5	X	X
Pseudomyrmex sp6	Ps6	X	X
Pseudomyrmex sp8	Ps8		X
Species richness		23	23
Shannon diversity		1.77	2.13
Carmargo evenness		0.26	0.34
Berger–Parker dominance		0.59	0.37

palmadora and *S. auriculatum* were the most visited during the dry season (64% of observations) and those of *S. langsdorffii*, *S. auriculatum* and *Aechmea aquilega* (Salisbury) were the most visited during the green season (41% of observations).

3.2. Temporal overlap

Among species with ≥5 observations during a season, temporal overlap (Schoener's index) varied from 0.17 to 0.69 during the dry season (Table 2), and varied from 0.35 to 0.87 during the green season (Table 2). The two most abundant ant species (*C. blandus* and *C. pusillus*) exhibited the greatest overlap during each season (Table 2). None of the pair-wise comparisons exhibited significantly different temporal activity patterns during either season (Table 2). Average pair-wise overlap in temporal activity was greater during the green season (0.57) than during the dry season (0.38). Of the species that were recorded at least 5 times each season, only *C. blandus* exhibited seasonal differences in temporal activity (Kolmogorov–Smirnov 2-sample test, $p = 0.024$; Fig. 1B).

Temporal overlap for the common flower-visiting ant assemblage during the dry season was no different than that expected by chance (Pianka = 0.442, $p = 0.162$; Czechanowski = 0.384,

Table 2
Dietary and temporal niche overlap (Schoener index) between pairs of species of ants using flower resources in the tropical semi-arid environment of the Brazilian Caatinga during the dry season (lower triangle) and during the green season (upper triangle). None of the Kolmogorov–Smirnov 2-sample tests evaluating pair-wise differences in dietary niches of ant species were significance ($p > 0.05$). Ant codes as in Table 1.

Dietary niche overlap

Ant species	Ant species						
	Cbl	Cpu	Pss	Cec	Cre	Cr2	Ppa2
Camponotus blandus	–	0.441	0.363	0.243	–	0.432	0.062
Cephalotes pusillus	0.626	–	0.489	0.458	–	0.533	0.333
Pseudomyrmex schuppi	0.465	0.694	–	0.333	–	0.444	0.111
Cephalotes clypeatus	0.442	0.516	0.333	–	–	0.250	0.375
Crematogaster sp1	0.442	0.516	0.333	0.800	–	–	–
Crematogaster sp2	–	–	–	–	–	–	0.250
Pseudomyrmex sp1	–	–	–	–	–	–	–

Temporal niche overlap

| Ant species	Ant species						
	Cbl	Cpu	Pss	Cec	Cre	Cr2	Cre
Camponotus blandus	–	0.706	0.673	0.556	–	0.673	0.387
Cephalotes pusillus	0.584	–	0.676	0.583	–	0.650	0.533
Pseudomyrmex schuppi	0.302	0.683	–	0.347	–	0.875	0.486
Cephalotes clypeatus	0.526	0.387	0.167	–	–	0.375	0.525
Crematogaster sp1	0.372	0.290	0.333	0.200	–	–	–
Crematogaster sp2	–	–	–	–	–	–	0.450
Pseudomyrmex sp1	–	–	–	–	–	–	–

$p = 0.053$; Fig. 2A). In contrast, during the green season was significantly greater than expected by chance (Pianka = 0.686, $p < 0.0001$; Czechanowski = 0.558, $p < 0.0001$; Fig. 2B).

4. Discussion

Although species richness of flowering plants visited by ants increased by 50% from the dry season to the green season, this increase in the availability of floral resources did not affect ant richness, which was the same in both seasons (23 species). Nonetheless, Shannon diversity increased and Berger–Parker dominance decreased during the green season, and ant species composition was highly season-specific, with 65% of the species occurring during only one of the two seasons. In the dry forest of Minas Gerais, Brazil, which is south of our study site and experiences similar seasonal changes to the Caatingas, ant richness was not affected by habitat heterogeneity (plant richness), by resource availability (plant density), or by season (Neves et al., 2010). Nonetheless, ant species composition in mature forests exhibited distinct differences between seasons. Ants in the Caatinga exhibited similar patterns to those in the dry forests of Minas Gerais with respect to both richness and composition (Table 1). Such seasonal variation in plant–ant interactions may reflect seasonal complementarity in plant use within ant guilds of dry tropical biomes. A similar pattern of seasonal complementarity occurs in tropical bees and wasps (Heithaus, 1979), which may represent an important niche axis for explaining increased richness of particular taxonomic groups in the tropics compared to their temperate counterparts.
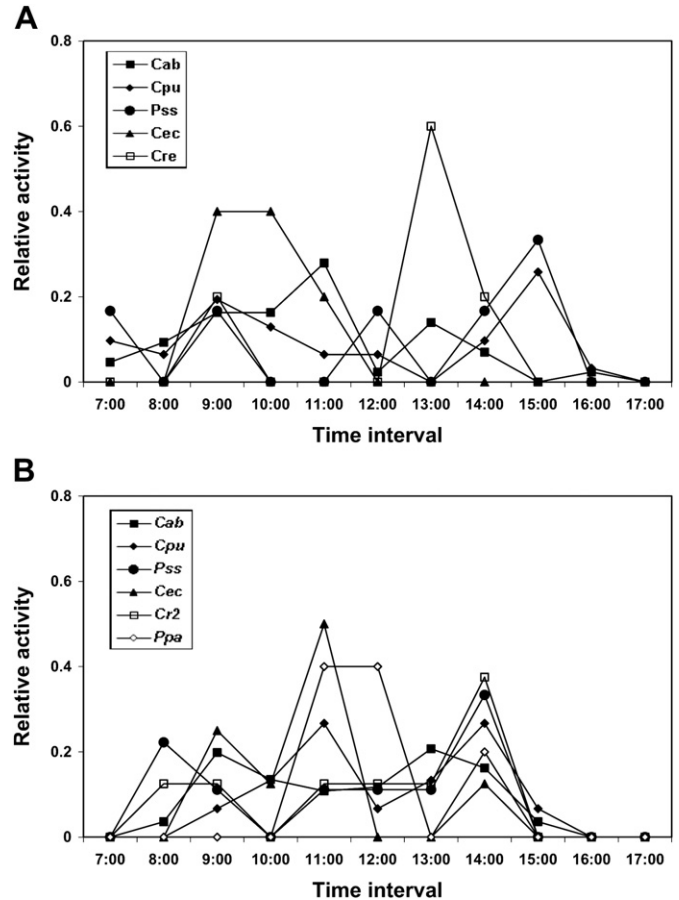
4.1. Trophic niche overlap

Floral resources are more abundant and diverse in the Caatinga during the green season than during the dry season (Santos et al., 2009; Vasconcellos et al., 2010) and during the green season more ants were recorded visiting a greater diversity of flowers compared to the dry season (Appendix A). The average number of individual ants recorded per flowering plant species was consistent
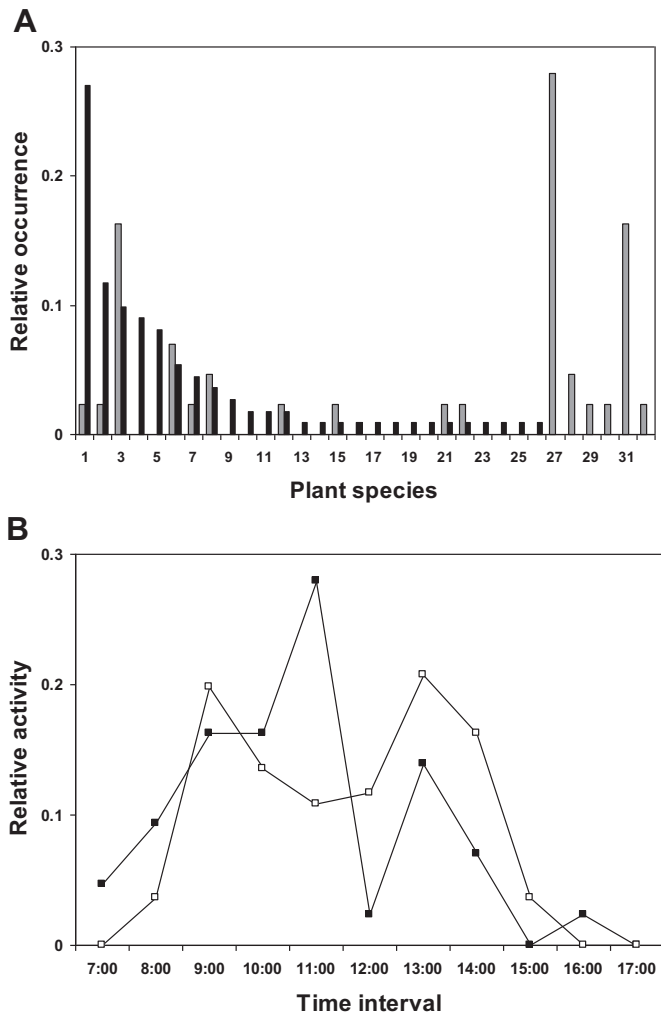
Fig. 1. Trophic niche profiles (A) and temporal activity patterns as percent of total activity (B) for *Camponotus blandus* during the dry season (black bars and ■) and during green season (gray bars and □) in the Brazilian Tropical dry forest.

Fig. 2. Temporal activity patterns (as percent of total activity) of flower-visiting ants from 07:00 to 17:00 h for the dry season (A) and for the green season (B), in the Brazilian Tropical dry forest.

regardless of season, with an average of 5.3 and 5.6 individuals captured per plant species during the dry and green seasons, respectively. This indicates that ant density on plants is relatively constant and that overall ant abundance may be affected by seasonal changes in phenology. In contrast, mean trophic breadth (i.e., average number of flower species visited per ant species) changed in concert with richness of flowering plants visited by ants. The number of flower species visited by ants increased by 50% from the dry season (22) to the green season (33), with mean trophic breadth also exhibiting a 50% increase from 2.5 to 3.7 species. This indicates that trophic niche breadth of flower-visiting ants is contingent on seasonal flower richness.

This seasonal trophic niche dynamic is made more complex by the season-specific composition of the flower-visiting ant guild in the Caatinga, as only 12 of 34 species were captured from flowers during both seasons. One may expect that the trophic structure of the assemblage would change between seasons simply because of changes in ant species composition. Nonetheless, seasonal changes in diet in response to changes in resource abundance and diversity, as well as changes in composition of the flower-visiting ant guild likely contribute to season-specific patterns of trophic niche over-lap. The most commonly captured species (*C. blandus*) evinced significant seasonal differences in the flowers it visited (Fig. 1A),

indicating that seasonal trophic niche shifts occur in this system. Species capable of seasonal dietary shifts in response to flowering phenology are less specialized than species that are not (Heithaus, 1979), suggesting that the 12 species captured from flowers during both seasons are likely to be trophic generalists compared to the 24 species that were captured only during the dry season or the green season.

Assemblage-wide dietary overlap was greater than expected by chance each season and pair-wise analyses failed to detect signifi-cantly different trophic niches between common species (Table 2). High dietary overlap of flower-visiting ants may indicate that particular plant species lack effective defenses against nectar theft by ants. Plants visited by more than 1/3 of ant species captured during each season that are likely to have poor defenses against nectar theft include, *I. pintoi* (visited by 11 ant species) and *T. pal-madora* (9 species) during the dry season, and *A. aquilega* (9 species), *S. langsdorffii* (8 species), *Senna macranthera* (8 species), and *S. auriculatum* (8 species) during the green season. The high degree of niche overlap each season suggests that competition is not a dominant force in structuring this ant guild, but that multiple ant species take advantage of the same poorly defended floral resources. Despite the fact that twice as many flower species were visited by a large proportion (>33%) of the ant guild during the green season compared to the dry season, trophic overlap was greater during the dry season (Table 2 and results of null model tests) because of the reduced abundance and diversity of resources. This paucity of floral resources could increase interspecific

competition, which should manifest as a decrease in trophic niche overlap during the dry season (Blüthgen and Fielder, 2004; Brown et al., 1981). Rather than this negative interaction, ant species in the Caatingas had greater trophic overlap during the dry season, indicating that competition for floral resources may not be an important mechanism for structuring this guild and that flower-visiting ant species shared common and abundant resources during each season.

4.2. Activity patterns and temporal overlap

Multiple forces may affect temporal activity patterns of flower-visiting ants, including physiological constraints associated with temperature and humidity, temporal variation in nectar production, and temporal variation in the production of barriers against nectar thieving ants (Blüthgen and Klein, 2011; Holland et al., 2011; Junker et al., 2011, 2007; Willmer et al., 2009). Because of shared evolutionary history of flower-visiting ants, if strong physiological constraints structure activity patterns, one would expect temporal overlap to be correlated with the intensity of the constraint. More specifically, physiological constraints would lead to greater temporal overlap during the hot and dry season than during the cooler, green season. Our results are in direct opposition to expectations based on a physiological constraints mechanism. Specific predictions about temporal overlap or temporal activity can not be made for mechanisms related to variation in the times of production of nectar and pollen or barriers to nectar theft, as any pattern could be produced depending on species-specific patterns of production by members of the plant assemblage and data are not available for the Caatinga.

The greater temporal overlap of flower-visiting ants observed during the green season (Table 2 and results of null model analysis) may be related to changes in the degree of coincidence in the temporal production of nectar or of floral barriers by plants. However, because many species of ants foraged on the same plant species, and because those plants appear to lack sufficient defenses against nectar theft (see above discussion on trophic niche overlap), temporal patterns of nectar production may be a more likely explanation for high temporal niche overlap. The trophic niche axis changed length (floral richness) and composition between seasons, whereas the length of the temporal niche axis is fixed and only the characteristics of particular times (e.g., diurnal patterns of change in environmental factors, temporal patterns of floral production) can change. C. blandus exhibited season-specific temporal activity patterns (Fig. 1B), which indicates that ant species are capable of changing behavior in response to environmental cues. The composition and species richness of flowers visited by ants changed greatly between the seasons (Appendix A). If the plants that flower during the green season produce nectar at more similar times of day during the green season than the plants that flower during the dry season, this would explain the change in temporal niche overlap among flower-visiting ants. Patterns of nectar production may be related to competition for pollinators (Bell et al., 2005), and not a response to the antagonistic relationship plants have with nectar thieving ants. Decreased abundance of resources during the dry season in the Caatinga (Aguiar et al., 1995; França et al., 1997) may result in fewer individuals and fewer species (Table 1) available to pollinate flowers (Blüthgen and Klein, 2011). As a result, plants may reduce competition for this limited resource (pollinators) during the dry season by producing nectar at different times of day (Bell et al., 2005; Mosquin, 1971), which would explain the random patterns of temporal niche overlap by flower-visiting ants during the dry season.

Future studies that measure patterns of nectar production, evaluate existence of barriers to nectar theft in plants, and consider the guilds of pollinators would clarify these complex relationships between plants and insects.

Appendix A. Supplementary material

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.jaridenv.2012.07.001.

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