The seasonal dynamic of ant-flower networks in a semi-arid tropical environment

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Abstract. 1. Several studies have recently focused on the structure of ecological networks involving ants and plants with extrafloral nectaries; however, little is known about the effects of temporal variation in resource abundance on the structure of ant–plant networks mediated by floral nectar.

2. In this study, it was evaluated how strong seasonality in resource availability in a semi-arid tropical environment affects the structure of ant–flower networks. We recorded ants collecting floral nectar during two seasons (from December 2009 to January 2013): dry and green seasons. Then, we built interaction networks for flower-visiting ants in the Brazilian Caatinga separately for each combination of transect and season.

3. In general, strong seasonality directly influenced patterns of ant–flower interactions and the overall complexity of these ecological networks. During the dry season, networks were more connected, less modular, and exhibited greater niche overlap of flower-visiting ants than during the green season. Moreover, resource utilisation by ants during the dry season tended to be more aggregated. These findings indicate that during the dry season, ant species tended to share many resource bases, probably owing to lower overall resource availability during this season. Species composition of the ant network component was highly season specific; however, a central core of highly generalised ants was present during both seasons.

4. The stability of this central core between seasons could strongly affect the ecological and evolutionary dynamics of these interaction networks. This study contributes to the understanding of the structure and dynamics of ant-flower interactions in extremely seasonal environments.

Key words. Caatinga, ecological networks, flower-visiting ants, modularity, nestedness, resource seasonality.

Introduction

Ants and plants interact in different ways, and studies focused on these interactions have made great contributions to our current understanding of ecological interactions (Bronstein *et al.*, 2006; Rico-Gray & Oliveira, 2007). Mutualisms involving ants and plants are among the most studied of all ecological interactions (Heil & McKey, 2003; Bronstein *et al.*, 2006), and such relationships can vary from facultative (e.g. those involving plants with

extrafloral nectaries) to highly specialised (e.g. those involving myrmecophyte plants) (Rico-Gray & Oliveira, 2007; Dáttilo *et al.*, 2013a).

In the tropics, the high diversity of mutualistic ant–plant interactions creates complex ecological networks of interactions (Guimarães *et al.*, 2006). In these ant-plant networks, plant and ant species are represented by nodes and their interactions are represented by links that describe the use of plant resources by ants (Guimarães *et al.*, 2006, 2007; Dáttilo *et al.*, 2014a). The topology of such networks is defined by the way in which interactions are distributed among species, and is useful for understanding the underlying structural

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processes of plant and ant assemblages (Bascompte *et al.*, 2003). Mutualistic networks involving ants and plants with extrafloral nectaries have recently been studied at the ecological community level from a network theory perspective, providing insights into ecological and evolutionary dynamics of interacting species (Guimarães *et al.*, 2006; Díaz-Castelazo *et al.*, 2010; Dáttilo *et al.*, 2013a). Importantly, the presence of ants on plants does not always involve mutualistic interactions (Rico-Gray & Oliveira, 2007). Ants can decrease plant fitness via damage to vegetative structures or by competing with effective pollinators for floral nectar (Galen, 1999; Ashman & King, 2005; Rico-Gray & Oliveira, 2007; Dáttilo *et al.*, 2012). Moreover, several studies have considered ants to be nectar 'thieves'; in these cases, because ants can obtain floral resources without pollinating flowers or providing other benefits to the plants (Puterbaugh, 1998; Dutton & Frederickson, 2012).

Although ants are often considered to be floral nectar thieves, floral nectar is an essential component of the diet of many of these ant species (Davidson *et al.*, 2003; Blüthgen *et al.*, 2004). However, nectar resources provided by plant reproductive structures are highly seasonal in space and time (Zimmerman, 1988; Rico-Gray, 1993), and most research on flower-visiting ants has addressed only specific ant–plant interactions or have been short-term studies, resulting in a knowledge gap regarding the seasonality of these interactions at the community level (Rico-Gray, 1989; Galen, 1999; Junker *et al.*, 2011; Dáttilo *et al.*, 2012).

The Brazilian Caatinga is one of the most important xeric morphoclimatic domains in South America and comprises arid and semi-arid vegetation formations over an area that covers about 700 000 km^2 (Sampaio, 1995; Prado, 2003). It is strongly seasonal with two well-defined seasons: a long dry season and a short rainy season (locally known as the 'green season'). This seasonality determines the spatial and temporal dynamics of resource productivity and availability in the Caatinga (Sampaio, 1995; Albuquerque *et al.*, 2012). Floral resources are more abundant and diverse in the Caatinga during the green season than during the dry season (Santos *et al.*, 2009, 2010; Vasconcellos *et al.*, 2010), resulting in increased diversity of ants attracted to those resources during this season (Lindsey & Skinner, 2001). Thus, seasonality in resource availability in the Caatinga has considerable potential to affect ecological interactions and to structure communities. More specifically, seasonality can greatly affect the nature and strength of ant–flower interactions in this semi-arid environment (Brito *et al.*, 2012).

In spite of the importance and increasing knowledge of the effects of temporal variation on the structure of ant–plant networks mediated by extrafloral nectar at the community level (Díaz-Castelazo *et al.*, 2010; Rico-Gray *et al.*, 2012; Lange *et al.*, 2013), no study has evaluated the structure of ant–flower networks and the seasonal dynamics of these networks. In this study, we evaluated the seasonal dynamics of ant–flower networks in a semi-arid tropical landscape in the Brazilian Caatinga. We hypothesised that as a result of the strong influence of seasonality on variation in the availability of resources for ants in the Caatinga, the structure of ant–flower networks would be temporally dynamic. More specifically, we predict that lower floral resource diversity and abundance during the

dry season would enhance niche overlap among ant species, because ants that feed on floral nectar would be obligated to share the fewer available resource bases (i.e. plant species) during this season. Consequently, high network connectivity and low modularity is expected during the dry season. In contrast, we predict that greater resource diversity and abundance during the green season will enhance niche differentiation in the ant community as higher quality resources are monopolised by competitively superior ant species (those with massive recruitment or aggressive behaviour; Dáttilo *et al.*, 2014b,c), whereas competitively inferior ant species would co-occur with dominant species only on plants that represent lower quality resources. This will result in less connectivity and greater modularity of the network during the green season.

Material and methods

Study area

We conducted this study in two areas of xeric deciduous scrub vegetation in the Milagres municipality, State of Bahia, northeastern Brazil (12°54′S, 39°51′W, elev. 480 m). The areas are located in the Caatingas morpho-climatic domain, which exhibits a tropical semi-arid climate. The region exhibits strong seasonality, with a long dry season from March and November and a short rainy season from December to February. We use the term 'green season' to designate the period immediately after the rains, when there are vegetation blooms, including massive flowering events. The mean, maximum, and minimum annual temperatures are 23.1, 28, and 19.1 °C, respectively. The mean annual rainfall is 460 mm, ranging from 137 to 1035 mm.

Sampling

To evaluate the seasonal dynamics of ant–flower networks in the Caatinga, we recorded ants collecting floral nectar during two seasons: dry and green seasons. During each sampling session, two collectors carefully and simultaneously inspected each flowering plant for flower-visiting ants along a 350 m long and 10 m wide transect. Transects were surveyed during daytime (from 08.00 to 18.00 hours), with six sampling sessions conducted during the dry season (two in July 2009, two in September 2009, and two in August 2012) and six sampling sessions during the green season (two in December 2009, two in February 2010, and two in January 2013). Each year, sampling was done approximately 2–3 weeks after the onset of rains, resulting in variation in the sampling months among years. This ensured that environmental conditions were similar among years. Moreover, sometimes when we arrived in the field the massive flowering event had not yet occurred. We did not sample the ant–flower interactions in 2011 because of logistical problems. However, we believe that the way the study was conducted is adequate to address the hypotheses in this paper, because we have true replicates and not subsamples or pseudo-replicates for both the dry and green season (the main aim of our study).

All ants observed foraging inside flowers were collected, and the number of ant individuals was recorded for each plant.

We did not differentiate among flowers on the same plant, with each plant considered to be a unit of observation. Ants were collected only from the surfaces of flowers and only after they were observed to forage on nectar. In this study, we considered an ant–flower interaction (ants feeding on floral nectar) only when ants were immobile, with mouthparts in contact with nectar secreting tissues, for periods of up to several minutes. Moreover, this behaviour is easily recognised in the field as nectar-feeding ants often have greatly distended gasters (Rico-Gray, 1993).

The identity of flowering plant species was recorded only for plants that were visited by ants (i.e. a complete vegetative survey of transects was not performed). To avoid under- and over-sampling, each flowering plant was inspected for exactly 5 min, regardless of the number of flowers per plants (method adapted from Sakagami *et al.*, 1967). This method is widely accepted and used in flower-visiting studies. Plants and ants were identified to the lowest possible taxonomic level, using taxonomic keys and the help of specialists. Vouchers were deposited in the Professor 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).

Network analysis

In order to test our hypothesis about the difference in the topological structure (i.e. the way in which interactions are distributed among species within an ecological network) of ant–flower networks between the dry and green seasons, we studied networks via the following metrics: number of ant–flower interactions, the mean number of ant and plant species, the number of interactions per species (degree), connectance, modularity, *C*-score, nestedness, network specialisation, species specialisation, and niche overlap. These network metrics provide a comprehensive characterisation of a network structure as well as a way to characterise the organisation of networks in a way that allows direct comparison among networks in this study and with previous work on ecological networks.

We calculated connectance (*C*) according to Jordano (1987), where $C = I/(A \times P)$, *I* is the total number of interactions observed, *A* is the number of ant species, and *P* is the number of plant species. Thus, connectance is defined as the proportion of total possible links that are realised in each network. We used the modularity index, *M* (range 0–1), to estimate the degree to which groups of species (ants and plants) interact more among each other than with species in other groups in the network (Newman & Girvan, 2004). High values of *M* indicate that the ants and plants form modules that are relatively independent of other interactions within the network (Olesen *et al.*, 2007). We calculated *M* using the MODULAR software (Marquitti *et al.*, 2014), and tested the significance of each observed *M* value with 1000 simulated networks generated by the Null Model II (CE) option (Bascompte *et al.*, 2003), in which the probability of an interaction occurring is proportional to the mean number of interactions of plant and ant species. Null model II is a conservative and biologically realistic test compared with other null models, and is commonly used in studies on

ecological networks. Deviations from this null model (i.e. significant results) result only from an asymmetric distribution of interactions between species. To determine if ant species exhibited patterns consistent with competitive exclusion, we used the co-occurrence index (*C*-score) (Stone & Roberts, 1990). This index is based on the average number of checkerboard units for each unique species pair (e.g. species 1 is present on plant A but not on plant B and species 2 is present on plant B but not on plant A) (range 0–1). Large *C*-scores indicate that species are highly exclusive and non-randomly distributed in the networks. Low *C*-scores indicate that the two species in question co-occur more often than would be expected by chance (Gotelli, 2000). We used the *NODF* metric (Almeida-Neto *et al.*, 2008) to estimate the nestedness value of the networks using the ANIN-HADO software (Guimarães & Guimarães, 2006). This metric ranges from 0 (no nestedness) to 100 (perfect nestedness). In a nested network, generalist species with many interactions (central core species of a network) have many interactions with each other, species with few interactions (specialists) interact with proper subsets of the central core of generalists, and few interactions occur between specialists (Bascompte *et al.*, 2003). We generated random matrices to test the significance of modularity and nestedness according to the null model described above using functions within the software MODULAR and ANIN-HADO. Network specialisation was estimated via the specialisation index (H_2') (Blüthgen *et al.*, 2006, 2007)*,* which measures interaction selectiveness at a network scale. This index is derived from the Shannon diversity of network links and is based on the deviation from the expected probability distribution of the interactions. In addition, we calculated the standardised specialisation index (*d'*) for each ant and plant species in each network (Blüthgen *et al.*, 2006, 2007). This index is derived from the Kulback–Leibler distance and calculates how the interactions of a species deviate from a random sampling of interactions with potential partners. Both indices of specialisation are quantitative and robust to changes in sampling intensity and network size, and range from zero (extreme generalisation) to one (extreme specialisation) (for additional details see Blüthgen *et al.*, 2006, 2007). We determined the dietary niche overlap of flower-visiting ants using Horn's index (Krebs, 1999). This index is less subject to bias associated with the number of resource categories, sample size, or resource unevenness compared with other indices. Horn's index varies from 0, when there is no overlap of resources, to 1, when there is complete resource overlap.

We characterised the central core of highly interacting species in each network for both ants and plants using the formula: $G_c = (k_i - k_{mean})/\sigma_k$, where k_i = mean number of interactions for a species *i*, k_{mean} = mean number of interactions for species in the network, and σ_k = standard deviation of the number of interactions for species in a trophic level (Dáttilo *et al.*, 2014b). Species with $G_c > 1$ have more interactions than other species of the same trophic level, and are considered to be species that comprise the generalist core of highly interactive species.

We used the R-software version 2.13.2 and the bipartite package (Dormann *et al.*, 2009) to calculate networks metrics and to construct bipartite graphs. To test for seasonal differences

(dry vs. green) based on each metric, we used paired *t*-tests conducted in R (R Development Core Team, 2010).

Results

We recorded 34 ant species feeding on nectar from 42 plant species (Tables 1 and 2). During the dry season, we observed 23 ant species interacting with 22 plant species ($n = 189$ interactions) (Fig. 1a). During the green season, we observed 23 ant species interacting with 32 plant species ($n = 335$ interactions) (Fig. 1b). The mean number of ant species per transect during the dry season was lower (mean $\pm$ SD: 9.67 ± 4.18) than during the green season (15.33 ± 4.59) ($t = -3.727$, d.f. $= 5$, $P = 0.014$) (Fig. 2a). Similarly, the number of plant species visited by ants per transect was lower during the dry season (8.67 ± 1.75) than during the green season (15.67 ± 1.03) ($t = -7.246$, d.f. $= 5$, $P < 0.001$) (Fig. 2b). In spite of these seasonal differences, the number of interactions per plant and ant species remained unchanged between seasons (Dry: 1.13 ± 0.23; Green: 1.19 ± 0.12; $t = 0.756$, d.f. $= 5$, $P = 0.484$). Moreover, 32.35% ($n = 11$) of ant species were observed during both seasons, with 28.57% ($n = 12$) of plant species visited by ants during both seasons.

Ecological ant–flower networks were more connected during the dry season (mean $\pm$ SD: $C = 0.27 \pm 0.03$) than during the green season ($C = 0.16 \pm 0.03$) ($t = 8.803$, d.f. $= 5$, $P = 0.001$) (Fig. 2c). This difference in connectivity reflected variation in dietary overlap, niche overlap of flower-visiting ants was greater during the dry season (Horn's index: 0.48 ± 0.11) compared with the green season (Horn's index: 0.35 ± 0.12) ($t = 3.474$, d.f. $= 5$, $P = 0.018$) (Fig. 2d). However, network specialisation was not significantly different between seasons (Dry season, $H_2' = 0.21 \pm 0.16$; Green season, $H_2' = 0.31 \pm 0.15$; $t = -1.103$, d.f. $= 5$, $P = 0.320$) (Fig. 2e). Ant species exhibited significantly less exclusion (i.e. not co-occurring on the same plant species) during the dry season (*C-score*: 0.34 ± 0.14) than during the green season (*C-score*: 0.50 ± 0.09) ($t = -3.128$, d.f. $= 5$, $P = 0.026$) (Fig. 2f).

Evaluating non-random patterns of ant–flower interaction within each network and season, no network was significantly modular when compared with the respective randomly generated null distributions of ant–flower interactions (all *P*-values > 0.05). Nonetheless, networks during the dry season tended to be less modular ($M = 0.41 \pm 0.05$) than during the green season ($M = 0.50 \pm 0.03$) ($t = -3.330$, d.f. $= 5$, $P = 0.021$) (Fig. 2g). In addition, ant–flower networks were significantly nested more often during the green season (four of six transects) than during the dry season (two of six transects). However, NODF-values were not significantly different between seasons (Dry, NODF $= 19.18 \pm 6.77$; Green, NODF $= 14.39 \pm 4.45$; $t = 2.223$, d.f. $= 5$, $P = 0.077$) (Fig. 2h).

For the combined data from all six transects, ant species composition that constituted the central core of highly interacting species remained unchanged between seasons; however, the proportion of species constituting the core and the periphery differed among transects. For example *Camponotus blandus* (Smith) was recorded on 100% of transects during each season,

whereas *Cephalotes pusillus* (Klug) was recorded from 50% to 83.33% of transects during the dry and green seasons, respectively. For plants, the number of species found in the generalist core varied from one to three plant species per transect. Moreover, the identity of the plant species in the generalist core substantially changed between seasons. The plant species generalist core during the dry season included *Ipomoea pintoi* O'Donnel (33.33% of transects), *Tacinga palmadora* (Britton & Rose) N.P. Taylor & Stuppy (33.33%), *Indigofera suffruticosa* Mill. (16.66%), *Stigmaphyllon auriculatum* A. Juss. (16.66%), and *Turnera cearensis* Urb. (16.66%). During the green season, plant species in the generalist core included *Senna macranthera* (DC. ex Collad.) H.S. Irwin & Barneby (100%), *Aechmea aquilega* (Salisb.) Griseb. (66.66%), *S. auriculatum* (33.33%), *Dioclea grandiflora* (Mart.) (16.66%), and *Senegalia langsdorfii* (Benth.) (16.66%). Only *S. auriculatum* was present in the generalist core during both seasons.

Discussion

In general, results supported our hypothesis that low resource diversity and abundance during the dry season enhanced niche overlap and co-occurrence among flower-visiting ants. In contrast, greater resource diversity and abundance during the green season may account for ant species being highly exclusive (*i.e.,* lower co-occurrence among species), with increased niche differentiation in the ant community. There was a great deal of seasonal turnover in the identity of ant species and plant species in the ant-flower interaction network (Tables 1 and 2). Only 12 of 34 ant species and 12 of 42 plant species were part of the network during both seasons. Only one plant species (*S. auriculatum*) was a member of the generalist core both seasons, with eight other species being core members during only one season. In contrast, the central core of highly interacting ant species comprised the same two species each season. Variation in phenology could explain the seasonal differences in plant membership to the generalist core of the network. *Camponotus blandus* and *C. pusillus* appear to be the only abundant ants in the Caatinga that make year-around use of a large diversity of floral resources. Interestingly, this central core of highly interacting ant species is the same as that found by Lange *et al.* (2013) in ant–plant networks mediated by extrafloral nectar in a Brazilian Savanna study located about 1185 km from our study area. In the Brazilian Savanna, this generalist core was stable over 19 months. This finding indicates that different geographically distant plant populations can intensively interact with the same ant species regardless of variation in environmental factors (e.g. rainfall, temperature, and vegetation physiognomy) or the type of interaction (mutualism or antagonism). In fact, the temporal and spatial stability of some ant–plant interactions may result from coevolutionary relationships, with convergence of traits by species from both sides of the interaction (Bascompte *et al.*, 2003; Thompson, 2005), with important implications for ecological and evolutionary dynamics in these networks (Thompson, 2005; Guimarães *et al.*, 2011).

Species richness, network connectivity, co-occurrence of ant species, niche overlap, and modularity all exhibited significant

Table 1. Ant species recorded feeding on floral nectar and the level of specialisation (d') (mean $\pm$ SD) in the Milagres municipality, State of Bahia, northeastern Brazil, during the dry and green seasons.

		Specialisation (d')	
Ants	Code	Dry season	Green season
Dolichoderinae			
Azteca sp1	Azt	0.56 ± 0.00	–
Linepthema sp1	Lin	0.54 ± 0.00	–
Ectatomminae			
Ectatomma muticum	Ect	–	0.17 ± 0.20
Gnamptogenys sp1	Gna	–	0.46 ± 0.00
Formicinae			
Brachymyrmex sp1	Bra	0.10 ± 0.00	–
Camponotus blandus	Cbl	0.19 ± 0.09	0.42 ± 0.12
Camponotus sp2	Ca2	0.28 ± 0.40	0.46 ± 0.00
Camponotus sp3	Ca3	0.41 ± 0.00	–
Camponotus sp7	Ca7	–	0.42 ± 0.15
Camponotus sp8	Ca8	–	0.46 ± 0.01
Camponotus sp9	Ca9	–	0.23 ± 0.18
Camponotus sp12	C12	–	0.49 ± 0.50
Nylanderia sp1	Nyl	0.01 ± 0.00	–
Pseudomyrmicinae			
Pseudomyrmex schuppi	Pss	0.10 ± 0.12	0.43 ± 0.05
Pseudomyrmex sp1 gp *pallidus*	Ppa	0.32 ± 0.00	0.29 ± 0.17
Pseudomyrmex sp2 gp *pallidus*	Pp2	0.30 ± 0.00	0.22 ± 0.07
Pseudomyrmex sp3	Ps3	0.21 ± 0.16	0.57 ± 0.26
Pseudomyrmex sp4	Ps4	0.16 ± 0.18	–
Pseudomyrmex sp5	Ps5	0.01 ± 0.00	0.57 ± 0.00
Pseudomyrmex sp6	Ps6	0.52 ± 0.16	0.21 ± 0.13
Pseudomyrmex sp8	Ps8	–	0.22 ± 0.11
Myrmicinae			
Acromyrmex sp1	Acr	–	0.69 ± 0.00
Atta rubropilosa	Att	–	1.00 ± 0.00
Cephalotes clypeatus	Cec	0.13 ± 0.10	0.19 ± 0.09
Cephalotes depressus	Ced	0.42 ± 0.00	0.15 ± 0.25
Cephalotes minutus	Cem	–	0.66 ± 0.16
Cephalotes pilosus	Cep	0.01 ± 0.00	–
Cephalotes pusillus	Cpu	0.20 ± 0.16	0.34 ± 0.34
Crematogaster sp1	Cre	0.35 ± 0.12	–
Crematogaster sp2	Cr2	0.64 ± 0.00	0.33 ± 0.14
Pheidole sp1	Phe	1.00 ± 0.00	–
Pheidole sp2	Ph2	0.63 ± 0.00	–
Pheidole sp3	Ph3	–	0.36 ± 0.43
Solenopsis sp1	Sol	0.54 ± 0.00	–

seasonal differences. These differences may be explained in part by the great amount of seasonal turnover among the members of the network. Nonetheless, the same mechanisms responsible for seasonal variation in ant–flower network composition may also be responsible for the seasonal differences in the structure of the networks. Indeed, factors that affect resource availability are important structuring mechanisms for ecological networks involving ants and plants (Rico-Gray *et al.*, 2012; Dáttilo *et al.*, 2013c; Lange *et al.*, 2013). In spite of the fact that modularity was different between seasons, no network exhibited significant modularity. Rather, ant species were idiosyncratic with respect to the species of plants with which they have interactions in the network. Additionally, the degree of nestedness did not change between seasons, reinforcing the idea that the nested pattern is

an invariant property of the interactions involving ants and plants (Guimarães *et al.*, 2006).

In general, resource abundance and quality are highly seasonal in the Caatinga, with resources being scarce during the majority of the year and abundant and diverse during the short vegetative bloom of the green season (Santos *et al.*, 2009, 2010; Vasconcellos *et al.*, 2010; Brito *et al.*, 2012). This blossoming of vegetation results in an ant–flower network that is larger (more interactions), less connected, and more modular than the dry season network. In addition, ant species co-occur more and exhibit less niche overlap during the green season compared with the dry season. The majority of these seasonal differences can be explained by seasonal changes in productivity that allow for greater niche partitioning and

Table 2. Plant species on which ants foraged for floral nectar and the level of specialisation (d') (mean $\pm$ SD) in the Milagres municipality, State of Bahia, northeastern Brazil, during the dry and green seasons.

|		Specialisation (d')	
Plants	Code	Dry season	Green season
Acanthaceae			
Ruellia bahiensis	Rub	0.44 ± 0.62	–
Apocynaceae			
Mandevilla funiformis	Maf	0.20 ± 0.19	0.34 ± 0.23
Arecaceae			
Syagrus vagans	Syv	0.05 ± 0.00	0.10 ± 0.00
Asteraceae			
Vernonia chalybaea	Vec	–	0.10 ± 0.00
Blanchetia heterotricha	Blh	–	0.10 ± 0.00
Bignoniaceae			
Adenocalymma comosum	Adc	–	0.10 ± 0.17
Anemopaegma album	Ana	–	0.10 ± 0.00
Arrabidaea cinerea	Arc	–	0.68 ± 0.18
Boraginaceae			
Cordia curassavica	Coc	–	0.23 ± 0.21
Bromeliaceae			
Aechmea aquilega	Aea	0.28 ± 0.05	0.38 ± 0.23
Aechmea lingulata	Ael	0.20 ± 0.22	–
Unidentified sp1	Un1	–	0.43 ± 0.11
Cactaceae			
Tacinga palmadora	Tap	0.23 ± 0.15	–
Pereskia bahiensis	Peb	0.15 ± 0.13	0.42 ± 0.59
Commelinaceae			
Dichorisandra hexandra	Dih	–	0.45 ± 0.00
Convolvulaceae			
Ipomoea pintoi	Ipp	0.18 ± 0.13	–
Ipomoea incarnata	Ipi	–	0.10 ± 0.00
Jacquemontia cf. *evolvuloides*	Jae	0.75 ± 0.00	–
Euphorbiaceae			
Croton heliotropiifolius	Crh	–	0.74 ± 0.46
Jatropha sp1	Ja1	–	0.46 ± 0.50
Fabaceae			
Dioclea grandiflora	Dig	–	0.12 ± 0.14
Indigofera suffruticosa	Ins	0.01 ± 0.00	0.03 ± 0.00
Senegalia langsdorfii	Sel	0.01 ± 0.00	0.41 ± 0.25
Senna macranthera	Sem	0.08 ± 0.11	0.34 ± 0.21
Luetzelburgia sp1	Lu1	0.01 ± 0.00	–
Mimosa gemmulata	Mig	–	0.76 ± 0.00
Malpighiaceae			
Stigmaphyllon auriculatum	Sta	0.14 ± 0.17	0.10 ± 0.09
Amorimia rigida	Amr	0.05 ± 0.00	0.11 ± 0.00
Malvaceae			
Melochia betonicifolia	Meb	–	0.14 ± 0.00
Melochia tomentosa	Met	–	0.10 ± 0.00
Sida cordifolia	Sic	–	0.10 ± 0.00
Sida galheirensis	Sig	0.07 ± 0.08	0.25 ± 0.02
Sida ulei	Siu	–	0.10 ± 0.00
Sidastrum micranthum	Sim	0.28 ± 0.11	–
Nyctaginaceae			
Bougainvillea spectabilis	Bos	0.01 ± 0.00	–
Passifloraceae			
Passiflora cincinnata	Pac	–	0.10 ± 0.00
Poaceae			
Setaria setosa	Ses	0.01 ± 0.00	–
Portulacaceae			
Portulaca umbraticola	Pou	0.05 ± 0.00	0.10 ± 0.00
Rhamnaceae			
Ziziphus joazeiro	Zij	–	0.01 ± 0.00
Solanaceae			
Solanum stipulaceum	Sos	0.26 ± 0.37	0.76 ± 0.00
Turneraceae			
Turnera cearensis	Tuc	0.20 ± 0.28	–
Verbenaceae			
Lippia pohliana	Lip	–	0.10 ± 0.00
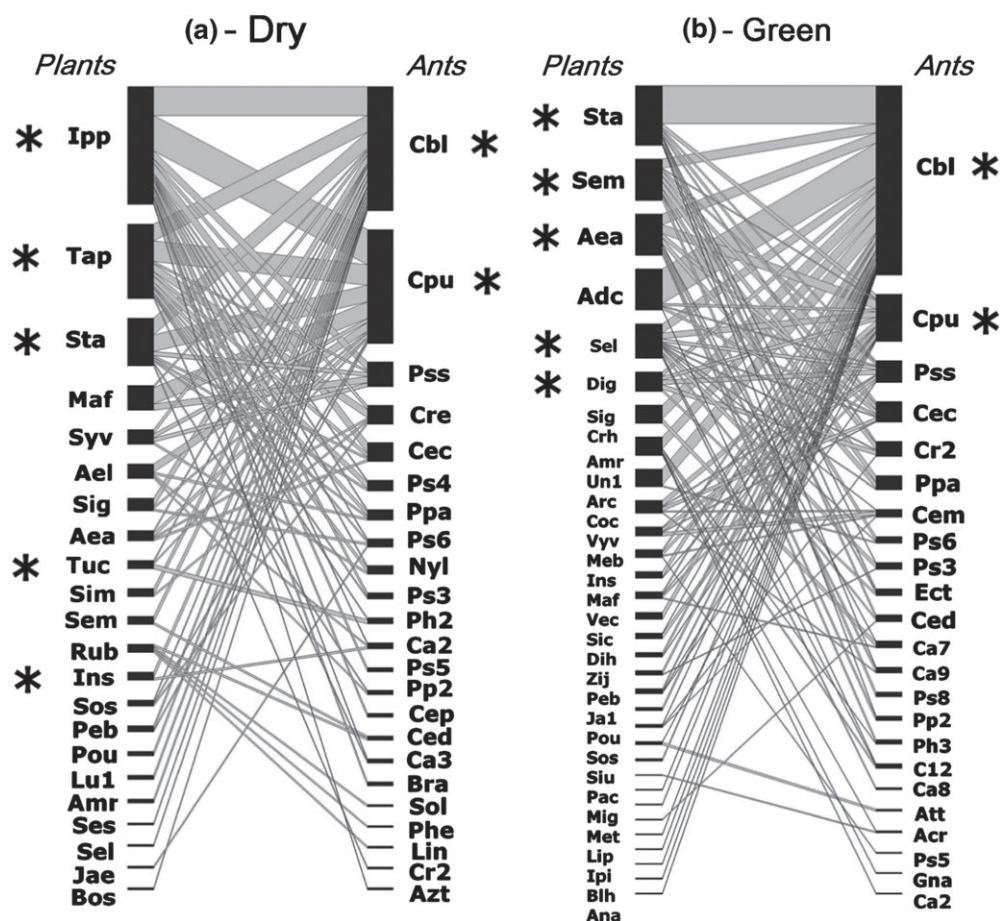
Fig. 1. Ant–plant interaction networks in the Milagres municipality, State of Bahia, northeastern Brazil, during the (a) dry and (b) green seasons. Data were collected between July 2009 and January 2013. The nodes on the left represent plant species and the nodes on the right correspond to ant species. Lines represent ant–flower interactions. Rectangle height is proportional to the number of interactions of each species. Line width is proportional to the number of visits observed. Asterisks (*) denote ant or plant species that comprise the generalist core for at least one transect. Each interaction network is based on the combined data from six transects. Ant and plant codes are in Tables 1 and 2, respectively.

resource specialisation during times of high resource abundance. Fewer plant species offer floral resources during the dry season, which results in a smaller network and necessitates greater niche overlap if ant species are to coexist. Increased niche overlap results in higher connectance and lower modularity in the network. During the dry season resources may be of lower quality (Peres, 2000; Wojcik *et al.*, 2008), which can decrease the role of competitive exclusion by dominant ants. Indeed, ants compete more strongly for higher quality resources (Blüthgen & Fiedler, 2004). Nonetheless, nectar is only one component in the diet of ants, as ants that feed on nectar do not depend exclusively on it (Rico-Gray *et al.*, 1998; Rico-Gray & Oliveira, 2007; Schoereder *et al.*, 2010). A recent study in the Brazilian Caatinga (Brito *et al.*, 2012) also concluded that resource scarcity during the dry season increased niche overlap of flower-visiting ants. When resources are scarce and of poor quality, it is expected that coexistence among ants will increase because ants cannot effectively defend these resources (Blüthgen & Fiedler, 2004).

In summary, seasonality in the Brazilian Caatinga has important consequences for the structure of ecological networks involving flower-visiting ants, influencing species richness, connectance, and modularity as well as patterns of species co-occurrence, and trophic niche overlap. Nonetheless, the fact that the central core of highly interacting ant species in our study site was stable among seasons has important implications for ecological and evolutionary dynamics of these networks, because these ant species interact with essentially all nectar-producing plant species in the Caatinga. However, studies over large spatial and temporal scales are required to evaluate the long-term stability of these ant–flower networks, which may indicate the relative importance of nectar-thieving ants on the structure of ant–flower networks.
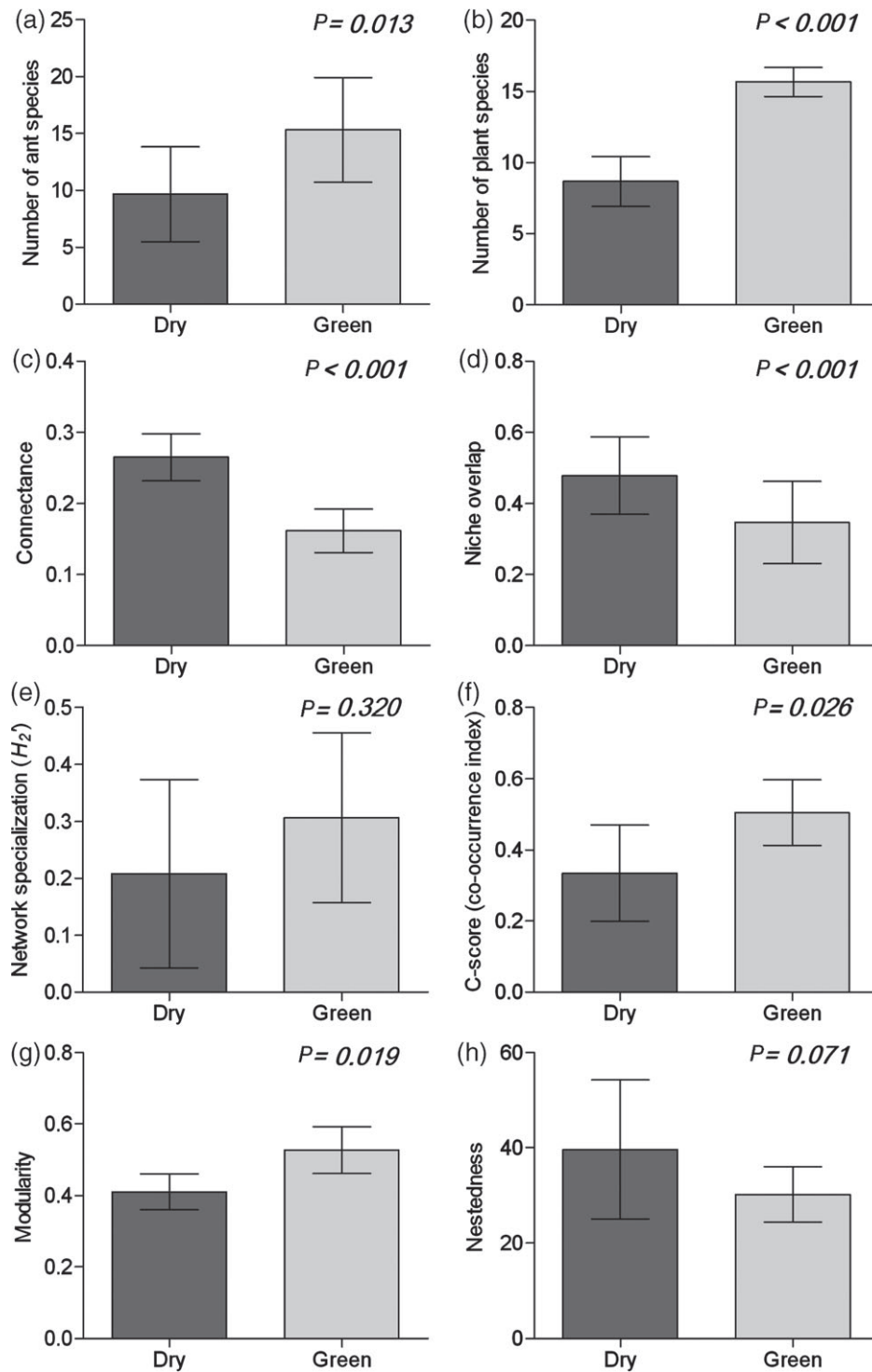
Acknowledgements

Fig. 2. Differences between ant–plant network properties during the dry and green seasons were tested with paired *t*-tests for: (a) number of ant species, (b) number of plant species, (c) connectance, (d) niche overlap of flower-visiting ants, (e) network specialisation, (f) co-occurrence, (g) modularity (*M*), and (h) nestedness (*NODF*). Each season is based on the combined data from six transects, and are represented as mean ± SD.

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