

Competition hierarchy and plant defense in a guild of ants on tropical *Passiflora*

F. F. Xu · J. Chen

Received: 25 June 2009 / Revised: 1 March 2010 / Accepted: 11 March 2010
© International Union for the Study of Social Insects (IUSSI) 2010

Abstract In facultative ant–plant interactions, ants may compete with each other for food provided by extrafloral nectar (EFN) plants. We studied resource competition and plant defense in a guild of ants that use the same EFN resource provided by two species of *Passiflora* in a seasonal rain forest in tropical China. At least 22 ant species were recorded using the EFN resource, although some of those species were rare. Among these ants, *Paratrechina* sp.1 and *Dolichoderus thoracicus* were more aggressive than other species. Ant aggressiveness measured as ant behavioral dominance index (BDI) was positively correlated with ant abundance on the *Passiflora* species studied. Ant BDI was also positively correlated to the protection that ants provided against herbivory. In *Passiflora siamica*, the number of workers patrolling on the plants did negatively correlate with average leaf loss per plant. We conclude that in this facultative *Passiflora*–ant system, plant defense upon herbivore was indeed influenced by the total number of ants present on plant and the aggressiveness of these ants.

Keywords EFN plant · Ant competition · Ant–plant mutualism · Plant defense · Competitive hierarchies

F. F. Xu · J. Chen (✉)
Key Laboratory of Tropical Forest Ecology,
Xishuangbanna Tropical Botanical Garden,
Chinese Academy of Sciences,
Mengla 666303, Yunnan, China
e-mail: cj@xtbg.org.cn

F. F. Xu
Graduate School of the Chinese Academy of Sciences,
Beijing 100039, China

Introduction

In ant–plant mutualisms, where plants provide food, or food and domatia in exchange for herbivore protection, some ants exclusively occupy their host plants because they are competitively superior (Palmer et al., 2000; Palmer et al., 2002). In facultative ant–plant interactions, many ant species utilize the same food resource, and competition may occur among them (de la Fuente and Marquis, 1999; Oliveira et al., 1999; Apple and Feener, 2001). Competitive interactions among ants on host plants may potentially shape the community structure of ant assemblages and affect plant defense against herbivores.

Several studies have shown that ant assemblages are often influenced by ants' competitive interactions, and that ant communities are highly hierarchical (Savolainen and Vepsäläinen, 1988; Andersen, 1995; Davidson, 1997; Bluethgen and Fiedler, 2004a). In most cases, competitively dominant ant species can be distinguished from competitively inferior species; and the distribution of the latter may be partly affected by the former (Savolainen and Vepsäläinen, 1988; Dejean and Corbara, 2003). Most studies of ant communities have also indicated that ant behavioral dominance usually coincides with abundance, and competitive hierarchies reflect the abundance rank of the particular ants in their community (Savolainen and Vepsäläinen, 1988; Andersen, 1995; Davidson, 1997; Bluethgen and Fiedler, 2004a, but see Leal et al., 2006). Interspecific competition among ants may also determine the degree of dietary overlap, where competitively dominant species exclusively occupy the most attractive food sources. Food that is lower in quality for dominant species is exploited by opportunistic subordinate species, which also share the resource

with other competitively inferior species (Blüethgen and Fiedler, 2004a, b).

Numerous studies on ant–extrafloral nectar (EFN) plant interactions indicate that most EFN plants attract many ant species simultaneously rather than interacting exclusively with a single species for their defense (de la Fuente and Marquis, 1999; Apple and Feener, 2001). The mechanism for ant species co-existence in the ant–EFN plant system has also been explored (Young et al., 1997; Palmer et al., 2000). Blüethgen et al. (2000) found that in an Amazonian rainforest canopy, competitively super ants usually dominate the most attractive food items while ants with lower competitive capacity share the less attractive EFNs (Blüethgen et al., 2000). Ant community that depends on honeydew and EFNs seems to be strongly shaped by competitive hierarchies (Blüethgen and Fiedler, 2004a). However, studies about the dominance hierarchy of ant species that shape ant assemblages on EFN host plants are still relatively scarce.

Different ant species provide a different quality of protection to their host plants (Suarez et al., 1998; Gaume and McKey, 1999; Giusto et al., 2001; Djiéto-Lordon et al., 2004; Ness et al., 2006). Morphological and behavioral differences, such as body size, colony size and aggressiveness can affect herbivore defense of the host plant (Gaume et al., 1997; Meunier et al., 1999). Gaume et al. (1997) suggested that the small body size of worker ants conferred a distinct advantage to the host plant in their study system. Rocha and Bergallo (1992) found that ant colony size was negatively correlated with herbivore damage. Palmer and Brody (2007) have suggested that more aggressive ant species provide better plant defense than less aggressive species, while one study on *Passiflora coccinea* get the opposite result (Leal et al., 2006). Nonetheless, more studies are necessary to better understand how different ant species and ant behavioral dominance index (BDI) influence plant defense against herbivores in facultative ant–plant mutualisms.

In this study, we propose that ant competitive hierarchies determine the division of resources from extrafloral nectaries among competing ants. Ant aggressiveness and abundance may affect on the quality of the herbivore defense provided by ants. Here, we ask the following questions (1) In a particular habitat, which ant species use EFN resources produced by two species of *Passiflora*? Which species dominate the resource and which are subordinate? (2) How aggressive are the ants present? Are the more aggressive ants more abundant? (3) Do aggressive ants provide a better herbivore defense than subordinates? (4) Are there correlations between ant BDI and ant abundance, ant numbers and average leaf loss per plant (which represents ant protection efficiency)?

Materials and methods

Study site

Our experiments were conducted in a ravine seasonal rain forest located in the Xishuangbanna Tropical Botanical Garden (21°41'N, 101°25'E, elevation 570 m), Chinese Academy of Science, China. Common plant species in the habitat include *Alchornea davidii* Franch., *Broussonetia papyrifera* (L.) L'Hér. ex Vent., *Macaranga denticulata* (Blume) Müll. Arg. (EFN), *Mallotus macrostachyus* (Miq.) Müll. Arg. (EFN), *Clerodendrum colebrookianum* Walp (EFN), *Gardenia sootepensis* Hutch., *Clerodendrum japonicum* (Thunb.) Sweet, *Mallotus paniculatus* (Lam.) Müll. Arg. (EFN), *Polygonum chinense* L., *Microstegium ciliatum* (Trin.) A. Camus, and *Camellia* sp. The climate is tropical to subtropical humid monsoonal, characterized by a distinct rainy season (May–October) followed by a cool dry season (November–February) and a hot dry season (March–April). Annual average temperature is 21.7°C, annual rainfall is about 1,500 mm, and annual relative humidity is 83%.

Study species

We used the two EFN-bearing plants *Passiflora siamica* Craib. and *Passiflora coccinea* Aubl. as model resource plants in this experiment. *Passiflora siamica* is native to the study site (Wu and Raven, 2007), and *P. coccinea* was introduced from Thailand in 1999. The two *Passiflora* species are very similar in many characters. Both are vigorous vines, having two glands on the leaf petiole and some glands on the undersides of leaves (*P. siamica*, 6.7 ± 2.8 per leaf, mean \pm 1SD, $n = 91$; *P. coccinea*, 7.4 ± 1.5 per leaf, $n = 104$). In *P. siamica*, glands on the leaf petiole are located in the middle or near the base; glands on the leaves are located in the middle. In *P. coccinea*, glands on the leaf petiole are at the base; glands on the leaves are along the border. During this experiment, neither of the plants were flowering.

Preparation of experimental plants

Experimental plants were propagated in a nursery from cuttings grown in pots. They were placed along the edge of the forest and in forest gaps in May 2008 when most shoots had reached a height of 30 cm. Ten sites located either in forest gaps or forest edges were chosen for the study, with more than 5 m between sites. Five individually potted plants for each species were placed at each site. Data for this study were mainly obtained from 40 plants (20 of each species) placed in the field among 10 sites (2 plants per site for each species). Following pot placement, ant species

were allowed to discover the plants for 1 month, after which time the number of ant species and total number of ant visitors to plants had stabilized as determined by censusing plants at 2-h intervals during the daytime for two non-consecutive days.

Census of ant species and abundance

Ants on the 40 plants were monitored once a week from 09:00 to 10:30 h (when the ants were most active) from June to November, 2008. A total of 17 censuses were taken. In each census, we identified and counted ants on each plant within a 30-s interval. A rapid on-site identification protocol for ant species was established from previous intensive observation. Most voucher specimens were taken before experimental censuses. For some rare species, voucher specimens were collected during the censuses. Ants taken as vouchers were alone and distant from other ants on the plant, so removal did not disturb other observations. Species identification was later confirmed from voucher specimens and identified by Prof. Zhenghui Xu (Southwest Forestry University).

Herbivore census

Herbivores attacking the plant species were also censused weekly. For identification, herbivores were photographed or collected near experimental plants, and occasionally from experimental plants. These herbivores were sent to Dr. Darong Yang (Xishuangbanna Tropical Botanical Garden) for identification.

Ant aggressiveness

All naturally occurring conflicts between ants were recorded on observation days other than those on which censuses were conducted. As conflicts among some ant species were uncommon, we artificially created opportunities for species to encounter each other. Plants that contained one species of ant were carefully placed adjacent to another plant that contained another species. Since many of the ant species created permanent or ephemeral nest in the pots, moving pots did not appear to influence the behavior of ants on the plant. After a short period of adaptation to the new environment, connections were made between the two plants by linking the coiling new tendrils of the two plants together. A small quantity of water was used to wash and remove a deterrent pheromone if an ant was observed hesitating when it was in another ant colony's territory. We did not wash the whole plant but only a small, relevant segment, about 5–10 cm of the plant tendrils. In this way, we created a new space between the two ant species' territories for which they could fight. This

portion of the experiment was carried out at the end of October, 2008.

Ant aggressiveness was assessed by calculating a BDI based on Santini et al. (2007). The number of times individual ants were dominant or subordinate was recorded for each pair of ant species that encountered each other. One individual was considered to be dominant if it behaved aggressively to the other and caused it to retreat. Aggressive behaviors included charging, biting or the use of chemical compounds from the tip of workers' gasters (Fellers, 1987; Bestelmeyer, 2000). Non-aggressive encounters between ant species were very rare and were excluded from analyses. Each of the encounters involved different ant pairs, and two encounters were separated in time to make sure that the result of one encounter did not affect another. Among the total 22 ant species we recorded on the *Passiflora* plants, for a subset of 7 we generated a complete matrix of pairwise BDI scores, with each pairwise score calculated from at least 10 encounters. Because the numbers of encounters between species pairs were not consistent across all pairs, we first calculated the proportion of dominant encounters in each species pair, and for each particular ant species the sum of the proportions of dominant encounter was divided by the number of ant species each ant species interacted with to obtain an average BDI of the ant species. This value is equal to the one calculated by dividing the number of dominant encounters by the total number of encounters when the numbers of encounters between species pairs are fixed. This average BDI value was used as an index of relative aggressiveness among the ant species.

Measurement of herbivory

Herbivore damage of each individual plant was determined by the average percent leaf loss measured 177 days after the plants were placed in the forest. The percent leaf loss per plant was estimated using digital photography and Photoshop 7.0 software to measure the proportion of leaf area lost or damaged by herbivores. Digital photographs were taken of every second leaf on a plant, starting from the youngest fully developed leaf closest to the terminal meristem. Care was taken to ensure the photograph was taken in the plane parallel to the leaf to avoid contorting the leaf shape. Total leaf area was measured as the number of pixels within a selected area which outlined the whole leaf in a photograph. For leaves missing areas along the margin, the original shape of the leaf was estimated by digitally rebuilding the lost area. Area of leaf loss was measured as the sum of pixels from selected areas around damaged or missing portions of the leaf, or missing areas along the leaf margin. Leaf loss (%) was calculated as the area of leaf lost (# of pixels) divided by total leaf area (# of pixels).

Approximately 10 leaves for each individual plant were measured.

For assessing herbivore damage, we used the proportion of leaf area damaged, rather than the total leaf area damaged, for two reasons. First, leaves are damaged at different growth stages; for example, a leaf that experiences 10% damage when small will retain 10% damage when it has reached maximum size. Therefore, 10% damage to a small leaf represents a significant loss even though the amount of leaf material damaged in absolute terms might be small. Second, the proportion of leaf area damaged is a better measure of the relative photosynthetic capacity lost to herbivory, thereby accounting for differences in leaf size and number among plants.

Data analysis

Pearson correlation was used to measure the correlation between ant species BDI and ant abundance. Linear regression was used to determine the relationship between the average proportional leaf loss from herbivory (arcsine square-root transformed) and the number of ants per *P. siamica* plant (square-root transformed). To address whether ant species with higher BDI provided greater protection against herbivory, we used the following procedure. First, to obtain a measure of protection provided by each ant species, we regressed the average proportional leaf loss (arcsine square-root transformed) against the abundance of each ant species (square-root transformed) separately, including the identify of the plant species as a categorical covariate. (We used univariate regressions rather than a single multivariate regression that included all ant species, because the size of the data set, 40 plants, did not support a multivariate regression with 8 independent variables, i.e., 7 ant species plus the plant species.) The resulting univariate regression coefficients thus measure the protection provided by each ant species. We then regressed these coefficients against the BDI of each ant species. Data were analyzed using SAS (v. 8.1).

Results

Species of ants

A total of 22 ant species was recorded on the *Passiflora* plants (Table 1). *Paratrechina* sp.1 *Dolichoderus thoracicus*, and *Tapinoma melanocephalum* were the most abundant ant species. Other common ant species included *Pheidole yeensis*, *Plagiolepis rothneyi*, *Paratrechina yerburyi* and *Diacamma rugosum* (Table 1).

Herbivory

The herbivorous insects observed were mainly generalists, including snails, katydids (*Pseudophyllidae*) and butterfly and moth larvae. *Passiflora coccinea* experienced lower herbivory (mean \pm SE, $1.4 \pm 0.4\%$) than *P. siamica* ($3.1 \pm 0.7\%$). Both species experienced relatively low herbivory during the study period.

Ant aggressiveness

Among the seven ant species tested, *Paratrechina* sp.1 and *D. thoracicus* were the most aggressive, having BDI scores of 0.87 and 0.86, respectively. The least aggressive ant species was *Paratrechina yerburyi* (BDI = 0.10, Table 2). Ant BDI was significantly positive correlated with species total abundance on plants (Pearson correlation, $r = 0.83$, $P = 0.02$, Fig. 1).

Relationship between ants and herbivory

In *P. siamica*, the average proportional leaf loss was negatively related to the total number of ants (regardless of ant species) present on the plant ($R_{\text{adj}}^2 = 0.18$, $P = 0.03$, $n = 20$), while for *P. coccinea* this relationship was not significant ($R_{\text{adj}}^2 = 0.07$, $P = 0.14$, $n = 20$) (Fig. 2). There was a statistically significant relationship between the protection that ants provided against herbivory and the ants' aggressiveness; the aggressive ant species with large BDI scores caused the greatest declines in herbivory ($R_{\text{adj}}^2 = 0.59$, $P = 0.03$) (Fig. 3).

Discussion

This study showed that ant species exhibited a dominance hierarchy in this facultative *Passiflora*-ant system, ant BDI was significantly correlated with the abundance of different ant species on plants. Many studies on the terrestrial ant community have shown that ant abundance was related to ant competitive capacity, where ant species with greater behavioral dominance have greater individual numbers (Savolainen and Vepsäläinen, 1988; Andersen, 1995; Davidson, 1997). However, rather few studies target on the relationship between the abundance and the aggressiveness of ant species in the facultative EFN plant ant system (but see Bluethgen and Fiedler, 2004a; Leal et al., 2006). The pattern in this study was somehow different to Leal et al. (2006), where a subordinate ant species was the second most abundant one. One explanation for this difference may be correlated to other EFN resources in the habitat studied. The most aggressive ant usually showed a

Table 1 Individuals (*n*) and relative abundance (%) of ant species visiting two EFN-bearing *Passiflora* species during 17 censuses of 30 s in a seasonal rainforest

Ant species	<i>Passiflora siamica</i>		<i>Passiflora coccinea</i>		Total	
	<i>N</i>	%	<i>N</i>	%	<i>N</i>	(%)
<i>Paratrechina</i> sp.1	209	20.4	424	32.7	633	27.3
<i>Tapinoma melanocephalum</i>	273	26.6	256	19.8	529	22.8
<i>Dolichoderus thoracicus</i>	284	27.7	213	16.5	497	21.4
<i>Pheidole yeensis</i>	39	3.8	243	18.8	282	12.2
<i>Plagiolepis rothneyi</i>	96	9.4	29	2.2	125	5.4
<i>Paratrechina yerburyi</i>	30	2.9	47	3.6	77	3.3
<i>Diacamma rugosum</i>	59	5.8	15	1.2	74	3.2
<i>Monomorium orientale</i>	21	2.1	35	2.7	56	2.4
<i>Pheidole roberti</i>	0	0	13	1.0	13	0.6
<i>Crematogaster rogenhoferi</i>	6	0.6	2	0.2	8	0.4
<i>Camponotus mitis</i>	0	0	6	0.5	6	0.3
<i>Camponotus singularis</i>	3	0.3	2	0.2	5	0.2
<i>Plagiolepis wroughtoni</i>	1	0.1	2	0.2	3	0.1
<i>Cardiocondyla wroughtonii</i>	0	0	3	0.2	3	0.1
<i>Paratrechina vividula</i>	0	0	2	0.2	2	0.1
<i>Tetramorium nipponense</i>	2	0.2	0	0	2	0.1
<i>Camponotus parius</i>	0	0	1	0.1	1	0
<i>Polyrhachis illaudata</i>	1	0.1	0	0	1	0
<i>Oecophylla smaragdina</i>	0	0	1	0.1	1	0
<i>Tetraponera allaborans</i>	0	0	1	0.1	1	0
<i>Crematogaster</i> sp.2	1	0.1	0	0	1	0
<i>Crematogaster</i> sp.3	1	0.1	0	0	1	0
Total	1026	100	1295	100	2321	100

Table 2 Number of interactions between pairs of ant species, with the number of interactions in which the row ant species was the dominant in parentheses, and the behavioral dominance index (BDI) for ant species visiting EFN-bearing *Passiflora* plants in a seasonal rainforest

Species	<i>DOTH</i>	<i>PHYE</i>	<i>TAME</i>	<i>DIRU</i>	<i>PLRO</i>	<i>PAYE</i>	BDI
<i>PASP</i>	21 (5) ^a	15 (15) ^a	16 (16) ^a	10 (10)	41 (41) ^a	14 (14) ^a	0.87
<i>DOTH</i>		15 (10) ^a	19 (17)	12 (11)	18 (17) ^a	23 (23)	0.86
<i>PHYE</i>			33 (21) ^a	15 (10) ^a	19 (17)	13 (10) ^a	0.55
<i>TAME</i>				17 (6) ^a	17 (17)	14 (11)	0.44
<i>DIRU</i>					22 (3)	14 (14)	0.37
<i>PLRO</i>						20 (17)	0.31
<i>PAYE</i>							0.10

^a Interactions were mostly (>50%) artificially created

PASP, *Paratrechina* sp.1; *DOTH*, *Dolichoderus thoracicus*; *PHYE*, *Pheidole yeensis*; *TAME*, *Tapinoma melanocephalum*; *DIRU*, *Diacamma rugosum*; *PLRO*, *Plagiolepis rothneyi*; *PAYE*, *Paratrechina yerburyi*

significant preference for nectar composition, they mainly visit those most attractive food items in the habitat (Blüethgen and Fiedler, 2004a, Blüethgen et al., 2000), but may also appear on the other EFN plants. A very aggressive ant *Oecophylla smaragdina* was recorded to visit two *Passiflora* plants in our *Passiflora*-ant system, but its

number was too low to be included in the BDI calculation. This ant might be mostly attracted by other food items in our study sites.

In this study, the degree of herbivore on each plant indicated by the average leaf loss was significantly correlated to the total ant numbers in *Passiflora siamica*, which

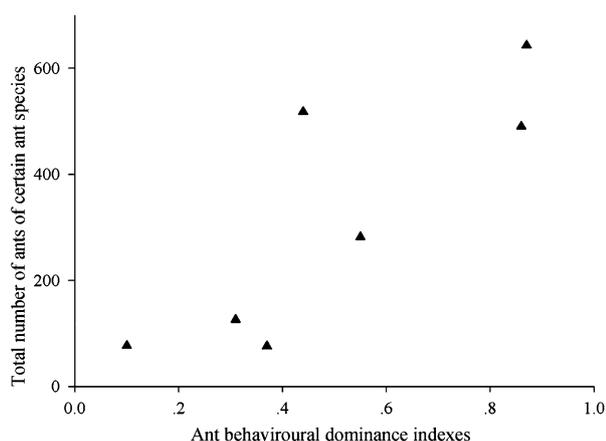


Fig. 1 The correlation between the behavioral dominance indexes (BDI) and ant abundance on two species of *Passiflora* (Pearson correlation coefficient = 0.83, $P = 0.02$, pooled data from 40 individual plants)

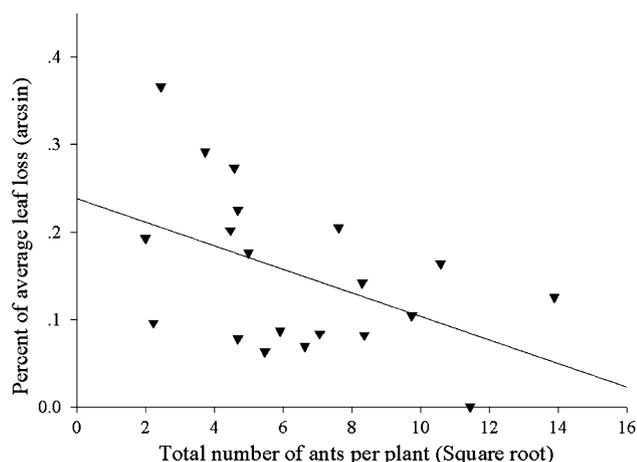


Fig. 2 Regression of the average proportional leaf loss per *P. siamica* plant (arcsine square-root transformed) against the total number of ants observed per plant (square root transformed) present ($R^2_{\text{adj}} = 0.18$, $P = 0.03$, $n = 20$)

suggests that total number of ants present on a plant is critical in determining the extent of ant protection. This result was in accordance with that in Rocha and Bergallo's study (1992), in which they showed that ant colony size was negatively correlated with herbivore damage. Total ant number of ants alone, without consideration of species can be an indicator of plant defense in *P. siamica* in our study. In the field, most EFN plants interact with more than a single ant species. In contrast, strictly obligate ant-plant mutualisms involving only a single ant species are rare (Rico-Gray and Oliveira, 2007). In this study, simultaneous occupancy of plants by multiple species of ants was common. EFN plants interacting with many ant species may benefit by associating with a greater number of species

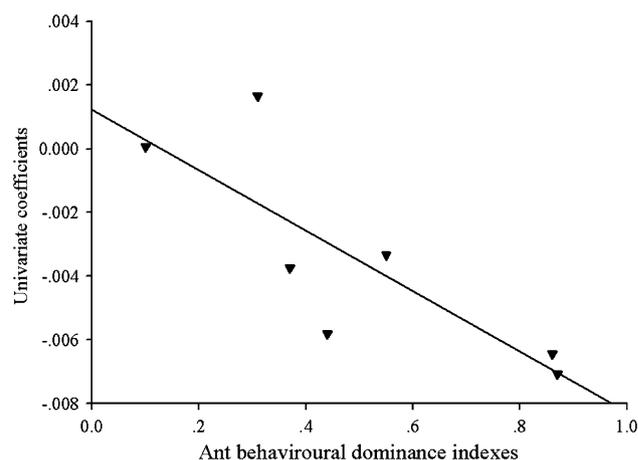


Fig. 3 The regression on the ant BDI against coefficients of seven ant species ($R^2_{\text{adj}} = 0.59$, $P = 0.03$)

since there is greater probability that in any given habitat, season, or time of day, some ant species will forage on the plant and be present to defend against herbivores (Rico-Gray and Oliveira, 2007).

Ant aggressiveness indicated by BDI appeared to play certain role in plant defense in this study, and ant BDI was significantly negative related to the univariate coefficients generated by regressions of average leaf loss of each plant and the number of each ant species present on that plant. This result was in support with Palmer and Brody (2007)'s, but not in agree with that of Leal et al. (2006). In an *Acacia*-ants system, Palmer and Brody (2007) found that more aggressive ant species provide better plant defense than less aggressive species, while Leal et al. (2006) found in their *Passiflora coccinea*-ants system that the subordinate ant species accounted for more attacks on simulated herbivore. One possible cause for this variation may be related to the feeding habit of the ants involved in the comparison, an ant species in prefer of protein food was more likely to attack the termite baits in Leal et al. (2006) study; they might not need to be the most aggressive ants. Other wise, other factors like disturbance, habitat condition, social structure of ant colonies and ant behavior may also affect the ant competition and colonization (Debout et al., 2009; Apple and Feener, 2001). Besides, whether ant aggressiveness can be a good indicator of a better plant defender needs further investigation.

Acknowledgments We thank Prof. Zhenghui Xu for identifying ants, Dr. Darong Yang for identifying other insects, Dr. Hong Wang for identifying plants in the habitat, Prof. Theodore Fleming, Dr. Matthew Warren for insight comments and help with language editing, Prof. Anthony R. Ives for advice in statistics, and Ms. Jianxiang Hu, Mr. Baogui Li, Mr. Xinming Li and Mr. Jianping Huang, Mr. Meng Li and Ms. Xiaomei He for field assistance.

References

- Andersen A.N. 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *J. Biogeography* **22**: 15-29
- Apple J.L. and Feener D.H. 2001. Ant visitation of extrafloral nectaries of *Passiflora*: The effects of nectary attributes and ant behavior on patterns in facultative ant-plant mutualisms. *Oecologia* **127**: 409-416
- Bestelmeyer B.T. 2000. The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. *J. Anim. Ecology* **69**: 998-1009
- Blüethgen N. and Fiedler K. 2004a. Competition for composition: Lessons from nectar-feeding ant communities. *Ecology* **85**: 1479-1485
- Blüethgen N. and Fiedler K. 2004b. Preferences for sugars and amino acids and their conditionality in a diverse nectar-feeding ant community. *J. Anim. Ecol.* **73**: 155-166
- Bliethgen N., Verhaagh M., Goitia W., Jaffé K., Morawetz W. and Barthlott W. 2000. How plants shape the ant community in the Amazonian rainforest canopy: the key role of extrafloral nectaries and homopteran honeydew. *Oecologia* **125**: 229-240
- Davidson D.W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biol. J. Linn. Soc.* **61**: 153-181
- Debout G.D.G., Dalecky A., Ngomi N.A. and McKey D.B. 2009. Dynamics of species coexistence: maintenance of a plant-ant competitive metacommunity. *Oikos* **118**: 873-884
- de la Fuente M.A.S. and Marquis R.J. 1999. The role of ant-tended extrafloral nectaries in the protection and benefit of a Neotropical rainforest tree. *Oecologia* **118**: 192-202
- Dejean A. and Corbara B. 2003. A review of mosaics of dominant ants in rainforests and plantations. In: *Arthropods of Tropical Forests: Spatio-Temporal Dynamics and Resource Use in the Canopy* (Y. Basset, V. Novotny, S.E. Miller and R.L. Kitching, Eds), Cambridge University Press, Cambridge. pp 341-347
- Djiéto-Lordon C., Dejean A., Gibernau M., Hossaert-McKey M. and McKey D. 2004. Symbiotic mutualism with a community of opportunistic ants: protection, competition, and ant occupancy of the myrmecophyte *Barteria nigritana* (Passifloraceae). *Acta Oecol.* **26**: 109-116
- Fellers J.H. 1987. Interference and exploitation in a guild of woodland ants. *Ecology* **68**: 1466-1478
- Gaume L. and McKey D. 1999. An ant-plant mutualism and its host-specific parasite: activity rhythms, young leaf patrolling, and effects on herbivores of two specialist plant-ants inhabiting the same myrmecophyte. *Oikos* **84**: 130-144
- Gaume L., McKey D. and Anstett M.C. 1997. Benefits conferred by "timid" ants: active anti-herbivore protection of the rainforest tree *Leonardoxa africana* by the minute ant *Petalomyrmex phylax*. *Oecologia* **112**: 209-216
- Heil M. and McKey D. 2003. Protective ant-plant interactions as model systems in ecological and evolutionary research. *Annu. Rev. Ecol. Syst.* **34**: 425-453
- Leal I.R., Fischer E., Kost C., Tabarelli M. and Wirth R. 2006. Ant protection against herbivores and nectar thieves in *Passiflora coccinea* flowers. *Ecoscience* **13**: 431-438
- Meunier L., Dalecky A., Berticat C., Gaume L. and McKey D. 1999. Worker size variation and the evolution of an ant-plant mutualism: Comparative morphometrics of workers of two closely related plant-ants, *Petalomyrmex phylax* and *Aphomyrmex afer* (Formicidae). *Insect. Soc.* **46**: 171-178
- Ness J.H., Morris W.F. and Bronstein J.L. 2006. Integrating quality and quantity of mutualistic service to contrast ant species protecting *Ferocactus wislizeni*. *Ecology* **87**: 912-921
- Oliveira P.S., Rico-Gray V., Diaz-Castelazo C. and Castillo-Guevara C. 1999. Interaction between ants, extrafloral nectaries and insect herbivores in Neotropical coastal sand dunes: Herbivore deterrence by visiting ants increases fruit set in *Opuntia stricta* (Cactaceae). *Funct. Ecol.* **13**: 623-631
- Palmer T.M. and Brody A.K. 2007. Mutualism as reciprocal exploitation: African plant-ants defend foliar but not reproductive structures. *Ecology* **88**: 3004-3011
- Palmer T.M., Young T.P. and Stanton M.L. 2002. Burning bridges: Priority effects and the persistence of a competitively subordinate acacia-ant in Laikipia, Kenya. *Oecologia* **133**: 372-379
- Palmer T.M., Young T.P., Stanton M.L. and Wenk E. 2000. Short-term dynamics of an acacia ant community in Laikipia, Kenya. *Oecologia* **123**: 425-435
- Rico-Gray V. and Oliveira P.S. 2007. *The Ecology and Evolution of Ant-plant Interactions*. The University of Chicago Press, Chicago. 123 pp
- Rocha C.F.D. and Bergallo H.G. 1992. Bigger ant colonies reduce herbivory and herbivore residence time on leaves of an ant-plant: *Azteca muelleri* vs. *Coelomera ruficornis* on *Cecropia pachystachya*. *Oecologia* **91**: 249-252
- Savolainen R. and Vepsäläinen K. 1988. A competition hierarchy among boreal ants: impact on resource partitioning and community structure. *Oikos* **51**: 135-155
- Santini G., Tucci L., Ottonetti L. and Frizzi F. 2007. Competition trade-offs in the organisation of a Mediterranean ant assemblage. *Ecol. Entomol.* **32**: 319-326
- Suarez A.V., De Moraes C. and Ippolito A. 1998. Defense of *Acacia collinsii* by an obligate and nonobligate ant species: the significance of encroaching vegetation 1. *Biotropica* **30**: 480-482
- Wu Z.Y. and Raven P.H. 2007. Clusiaceae through Araliaceae. In: *Flora of China. Vol. 13*, Science Press, Beijing. pp 141-149
- Young T.P., Stubblefield C.H. and Isbell L.A. 1997. Ants on swollen-thorn acacias: species coexistence in a simple system. *Oecologia* **109**: 98-107