



Variation of ant community structure on *Ficus benguetensis*

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ABSTRACT: Although ants are commonly found on *Ficus* trees, information remains lacking on the pattern and diversity of the ant community visiting these trees. We hypothesize that dynamic changes in the availability and types of food can affect the composition as well as abundance of ant communities occurring on fig trees. To investigate the impact of resource availability, diversity, and variability on the ant community structure, we surveyed and recorded the fig phenology and ant abundance on 17 trees (11 male and six female trees) of *Ficus benguetensis* in New Taipei City in northern Taiwan from 2011 to 2013. A total of 13 ant species were found on these fig trees, with 6 species more abundant than the others. The composition and relative abundance of the ant species occurring on *F. benguetensis* trees showed significant variations associated with tree sex, fig abundance, fig developmental phase, as well as temperature. A degree of dietary niche partitioning was also observed. We suggest that sexual differentiation in fig phenology plays a major role in controlling the availability and variance in food resources for ants, thereby shaping the complex ant communities foraging on *F. benguetensis*.

KEY WORDS: Ant community; Dietary niche partitioning, *Ficus*; Resource diversification.

INTRODUCTION

Ants are among the most abundant, diverse, and ecologically significant organisms in the tropics and subtropics (Davidson and Patrell-Kim, 1996; Davidson, 1997; Wilson and Hölldobler, 2005; Dejean *et al.*, 2010). They exploit a large array of resources and differ markedly in their feeding habits. Some tropical ants depend mainly on vegetal-derived nutrients, such as seeds, extrafloral nectar, food bodies, and honeydew from other insects (Davidson and Patrell-Kim, 1996; Davidson *et al.*, 2003; Blüthgen *et al.*, 2004), while others are predators or scavengers (Blüthgen and Stork, 2007; Sanders *et al.*, 2007). Recent studies confirmed the strong bottom-up effect of resource availability on the structure of ant communities (Blüthgen *et al.*, 2004; Sanders *et al.*, 2007). Although omnivory is considered widespread (Hunter, 2009), the quality and quantity of resources, often highly fluctuating, could influence the nature of plant-ant interactions (Heil *et al.*, 2005).

Ants are commonly found on a number of fig trees (*Ficus* spp., Moraceae) (Bain *et al.*, 2014a). As a tropical keystone species (Berg and Corner, 2005), *Ficus* species provide abundant and frequent food resources (Kuaraksa *et al.*, 2012; Bain *et al.*, 2014b) for a wide variety of vertebrate wildlife (Shanahan *et al.*, 2001) and insects, including ants (Martínez-Mota *et al.*, 2004). Although studies on the *Ficus*-ant relationship were recently reviewed by Bain *et al.* (2014a), little is known about the specific effect of fig resources on associated ant communities on *Ficus* trees. Nevertheless, ants are common on fig trees and have

been documented on approximately 11% of all *Ficus* species (Bain *et al.*, 2014a). The relationship between the plant and the ant, however, is less clear. The fig tree could provide diversified resources to ants, including food (e.g. nectar, wasps) or nest shelter. Certain fig species that have been observed providing shelter to arboreal ants (Maschwitz *et al.*, 1994; Bain *et al.*, 2012). Ants were observed to predate on wasps occurring on fig surface (Schatz *et al.*, 2006; 2008). In addition, it is suspected that some species secrete sugar for ants (Harrison, 2014). In return, ants may cause deleterious or beneficial effects on figs (Bain *et al.*, 2014a). Ants can be harmful to figs either indirectly by tending sap-sucking hemipteran insects (Bain *et al.*, 2012, 2014a) or directly by preying on pollinating wasp (Compton and Robertson, 1991; Schatz and Hossaert-Mckey, 2003; Schatz *et al.*, 2008). Conversely, they can benefit the *Ficus* plants in seed dispersal (Roberts and Heithaus, 1986; Martínez-Mota *et al.*, 2004), protection against herbivores (Novotny *et al.*, 1999), and deterrence of the non-pollinating fig wasps (Compton *et al.*, 2009).

However, fig resources can be highly variable not only between seasons, but also in terms of tree sex and fig developmental phases. Nearly half of the *Ficus* species are functionally dioecious: male trees produce pollen, fig wasps, and seedless figs whereas female trees exclusively produce figs with seeds (Patel *et al.*, 1995). In addition, given that pollinating wasps are unable to oviposit in female figs (Patel *et al.*, 1995) and the non-pollinating fig wasps (NPFWs) exclusively target male figs, the benefit to ants from figs may be

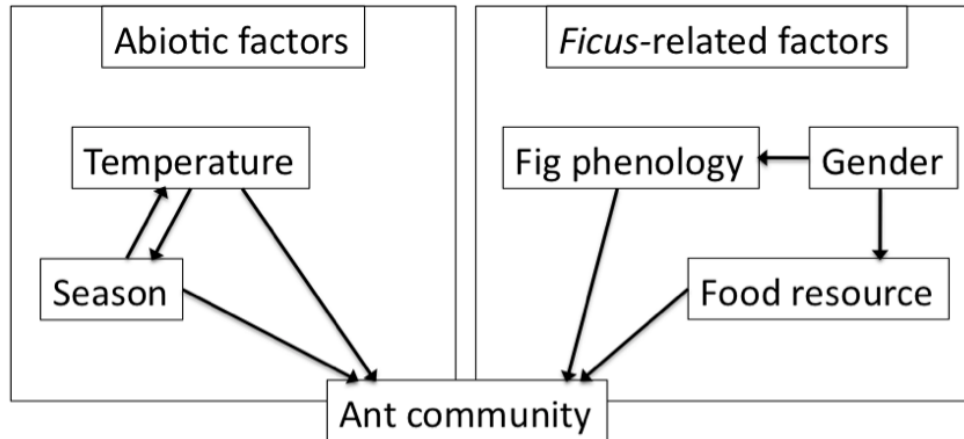


Fig. 1. Concept map of the different factors involved in the ant community structure.

different between tree sexes. Although honeydew secreted by hemipteran insects and sugars secreted by figs can present in both sexes of dioecious *Ficus* species, seeds can only be produced by female trees while wasps only present on male trees. The presence of both pollinating and non-pollinating fig wasps makes male figs a more favorable foraging option for predatory ants than female figs (Schatz *et al.*, 2008). The NPFWs, ovipositing from outside the fig, also spend more time on the surface of the male figs than pollinating wasps do. The resultant higher resource availability in both type and abundance thus contributes to greater diversity in the ant composition and greater ant abundance on male trees than on female trees. Additionally, the resource types available in figs continue to change throughout fig developmental phases, attracting ant species with differing nutrient requirements and feeding habits. We expect the increase in resource diversification could be reflected in the complex composition of the ant communities during the different fig developmental phases as well as between male and female fig trees.

In addition to resource availability, diversity, and variability, climate may be another factor influencing the structure of ant communities (Anderson, 1997). In many harvester ant species, foraging behaviors were found influenced by the temperature (Azcárate *et al.*, 2007) and varying between seasons (Brown and Gordon, 2000). Along with temperature, humidity has also been shown to influence the foraging behaviors of harvester ants (Gordon *et al.*, 2013) as well as those of leaf-cutting ants (Roces and Kleineidam, 2000).

In order to investigate the effect of the biotic (fig resources) and abiotic factors (temperature and rainfall) on the ant community pattern (Fig. 1), we conducted a two-year survey monitoring the diversity and abundance of ants. The factors related with fig resource include the sex of the fig tree, fig abundance, and fig developmental phase. The study aims to explore the

relationship between these factors and the abundance of ants and the species composition of the ant community

MATERIALS AND METHODS

Study species and site

Fieldwork was conducted in a secondary forest in Xindian District, New Taipei City (24°54'10"N, 121°33'31"E) in northern Taiwan. This location has a subtropical climate: during the study period, the annual rainfall was 3988.5 mm, and the mean weekly temperature ranged from 16.1°C in winter to 26.9°C in summer. These data were collected from the Quchi station of the Taiwan Central Weather Bureau, located three kilometers from the study site.

Ficus benguetensis Merrill (1905), distributed over the Ryukyu Islands, Taiwan, and the Philippines (Berg, 2011), is a functionally dioecious species belonging to the subgenus *Sycomorus*, section *Sycocarpus*. Thriving mainly in humid environments, this fig species can reach 15 m high, with figs growing on the trunk or on apical branches (Lin *et al.*, 2015). The phenology of *F. benguetensis* showed clear sexual differences in fig production. Not only did male fig production peak earlier and exhibit more production peaks per year than female production (Fig. 2), but male trees also showed a nearly continuous year-round fig production (Lin *et al.*, 2015).

In Taiwan, the pollinating wasp associated with *F. benguetensis* is the agaonid *Ceratosolen wui* (Chen and Chou, 1997). Of the four NPFW species that have been documented on *F. benguetensis* in Taiwan (Bain *et al.*, 2015), one NPFW species, *Philotrypesis* sp. (Hymenoptera: Pteromalidae: Sycoryctinae), was observed at the study site. Adult NPFWs oviposit from outside the figs, approximately 1-2 weeks after pollination, and their larvae parasitize agaonid pollinator larvae (Kerdelhué and Rasplus, 1996). We classified the fig developmental phases according to the categories established in Galil and Eisikowitch (1969).

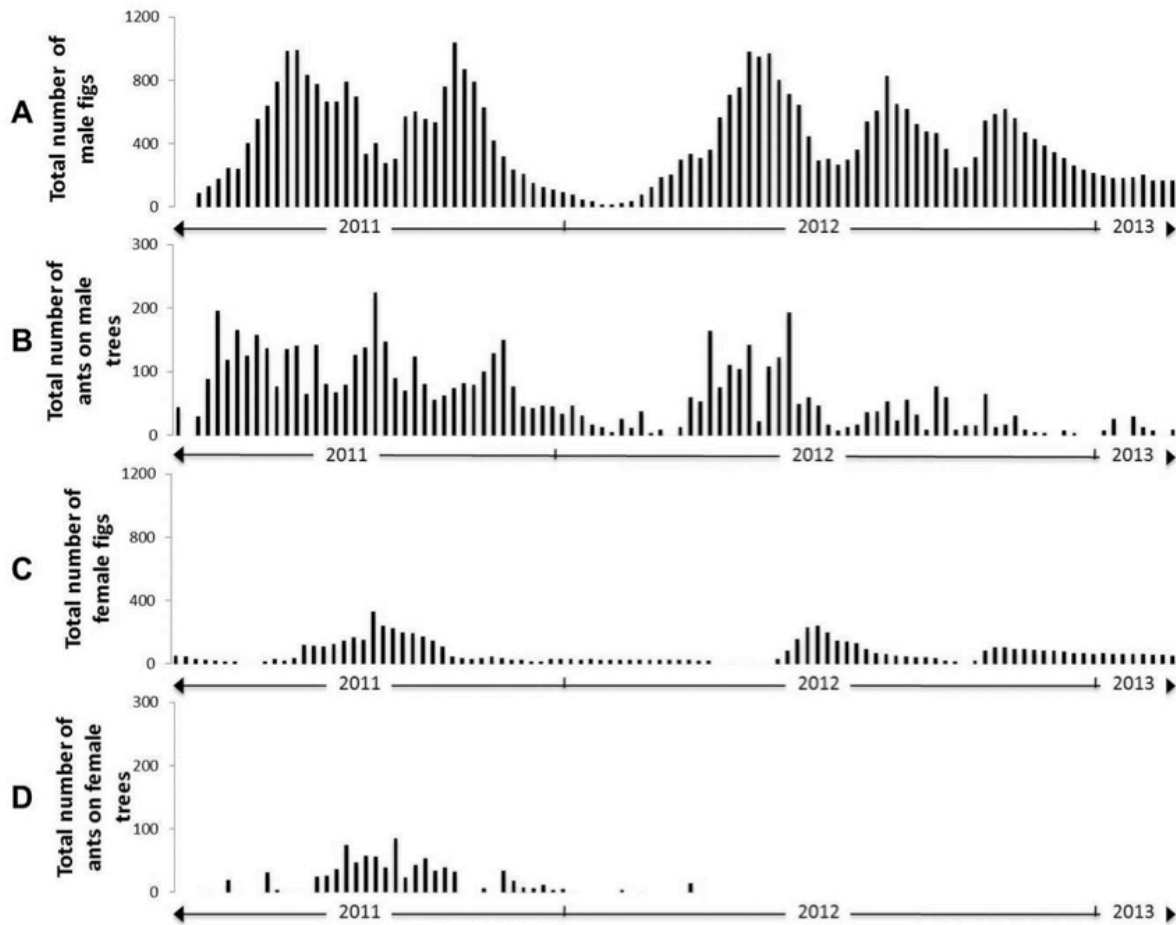


Fig. 2. The total number of figs on male (A) and female trees (C); total number of ants on male (B) and female trees (D).

Surveys

To avoid pseudo-replication within the territory of a single ant colony, observations from trees less than 8 m apart were not considered (Blüthgen *et al.*, 2004). Seventeen trees (11 male and six female trees) were monitored every week between March 2011 and March 2013 (102 surveys). As the male trees produced the majority of their figs on the trunk (Lin *et al.*, 2015), only a specific area of the trunk located between 120 and 150 cm high was monitored (Fig. 3A). During each survey, the number of figs and their developmental phases were recorded as well as the number of ants patrolling the observed area (ant abundance). Ant occurrence was the number of presence of each species during all observations. According to preliminary observations showing that ants are most active around noontime, ant surveys were conducted between 10 AM and 2 PM. Each tree trunk was monitored for approximately 2–5 min to obtain a “snapshot” of the ant activity. Ant specimens were collected and identified to the genus and species by using general and local identification keys (Bolton, 1994; Lin and Wu, 2003; Terayama, 2009).

Statistical analyses

After verifying the absence of autocorrelation in the time series of ant abundance through Durbin-Watson tests, Pearson correlation tests with application of Bonferroni correction for multiple comparisons were used to estimate the relationships between ant abundance and both abiotic (temperature and rainfall) and biotic (e.g., fig developmental phases) factors. Because the fig phenology of *F. benguetensis* is correlated neither to temperature nor to rainfall (Lin *et al.*, 2015), abiotic and biotic factors were considered as two independent sets of variables. There were three ways in data manipulation before correlation tests were conducted. First, we pooled total ant abundance of all trees by week (i.e., N = 102) for the correlation analysis between abiotic factors and fig abundance. Second, all observations (i.e., N = 1734 fig-surveys, including 1122 and 612 on male and female trees respectively) were used in the correlation analysis for biotic factors on fig abundance. Third, given the highly asynchronous fig production by *F. benguetensis* (trees bearing figs at different development phases: Lin *et al.*, 2015), we assigned the fig phase of each tree based on which

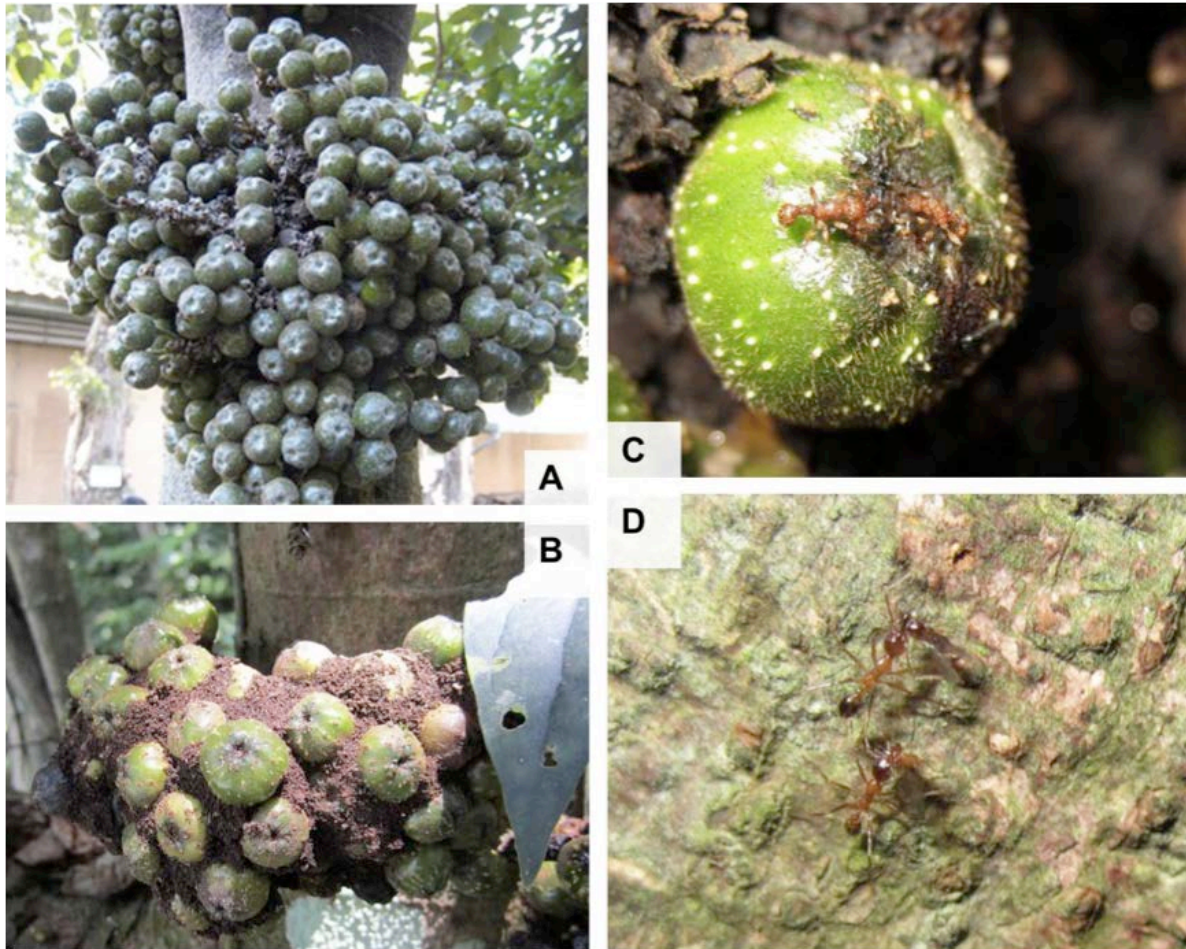


Fig. 3. Photos of *Ficus benguetensis*. **A:** Fig clusters on a male tree trunk on the National Taiwan University campus, Taipei, Taiwan. **B:** Nest of *Lophomyrmex taivanae* on a fig cluster. **C:** *Tetramorium nipponense* ants waiting at the ostiole of a male fig. **D:** Two *Lophomyrmex taivanae* workers grasping fig wasps in their mandibles.

phase represented more than 50% of the total number of observed figs (e.g., Trees in C-phase: N = 179, 39, 378 and 31 in A-, B-, C-, D-phase of male figs and 70, 20, 239 and 12 in A-, B-, C-, E-phase of female figs).

On account of the non-normality of the data, Kruskal-Wallis H tests were used to examine the differences between seasons in the composition of the ant community. Mann-Whitney U tests were also used to compare ant abundance between male and female trees and in the presence or absence of figs. The statistical analyses were performed using SYSTAT v12 (Systat Software, Inc., San Jose, California, USA).

RESULTS

Ant species composition and abundance

Over the 102 survey trips, we found ants occurring on all 17 fig trees. A total of 6253 workers belonging to 13 different genera and species were identified on male trees, and ten species were found on female trees (Table 1). The six most abundant species, representing more than 97% of

the total number of observed ants, included *Lophomyrmex taivanae* Forel, 1912; *Pristomyrmex punctatus* Smith, 1860; *Crematogaster subnuda formosae* Wheeler, 1909; *Pheidole noda noda* Smith, 1874; *Tetramorium nipponense* Wheeler, 1928; and *Technomyrmex albipes brunneus* Forel 1895. On male trees, the most abundant species was *Lophomyrmex taivanae*, representing 32.6% of the total number of observed ants. By contrast, *Pristomyrmex punctatus* was the most abundant species on female trees, representing 57.7% of the total number of ants observed on female trees (Table 1).

Abiotic factors

The total number of worker ants was positively correlated with the weekly mean temperature (Pearson correlation coefficient test: $R = 0.741$, $P < 0.01$) but not with the weekly rainfall. Moreover, the abundance of the six most common ant species showed significant seasonal variation (Kruskal-Wallis H test: $P < 0.01$; Fig. 2), with the number of observed species highest in summer, followed by that in spring (Fig. 4).



Table 1: Abundance (number of individuals) and occurrence (number of observations) of 13 ant species found on male and female trees of *F. benguetensis* (number of trees).

	Male			Female		
	Abundance (%) (n=5111)	Occurrence (%) (n=1122)	Trees (n=11)	Abundance (%) (n=1142)	Occurrence (%) (n=612)	Trees (n=6)
<i>Lophomyrmex taivanae</i>	1665(32.6)	77(6.86)	3	132(11.6)	11(1.80)	2
<i>Crematogaster subnuda formosae</i>	1032(20.2)	134(11.9)	10	40(3.50)	12(1.96)	4
<i>Pheidole noda noda</i>	770(15.1)	71(6.33)	5	140(12.3)	17(2.78)	2
<i>Pristomyrmex punctatus</i>	557(10.9)	35(3.12)	6	659(57.7)	28(4.58)	4
<i>Tetramorium nipponense</i>	489(9.57)	125(11.1)	10	64(5.60)	29(4.74)	5
<i>Technomyrmex albipes brunneus</i>	464(9.08)	105(9.36)	9	66(5.78)	15(2.45)	5
<i>Monomorium intrudens intrudens</i>	62(1.21)	10(0.89)	5	23(2.01)	3(0.49)	3
<i>Polyrhachis wolffi</i>	42(0.82)	37(3.30)	7	13(1.14)	13(2.12)	4
<i>Paratrechina yaeyamensis</i>	19(0.37)	2(0.18)	2	4(0.35)	1(0.16)	1
<i>Dolichoderus thoracicus</i>	4(0.08)	4(0.36)	4	1(0.09)	1(0.16)	1
<i>Pseudolasius binghami taivanae</i>	4(0.08)	4(0.36)	3	NA	NA	NA
<i>Tetraponera attenuata</i>	2(0.04)	2(0.18)	1	NA	NA	NA
<i>Odontomachus monticola</i>	1(0.02)	1(0.09)	1	NA	NA	NA

The six most abundant ant species are shown in boldface.

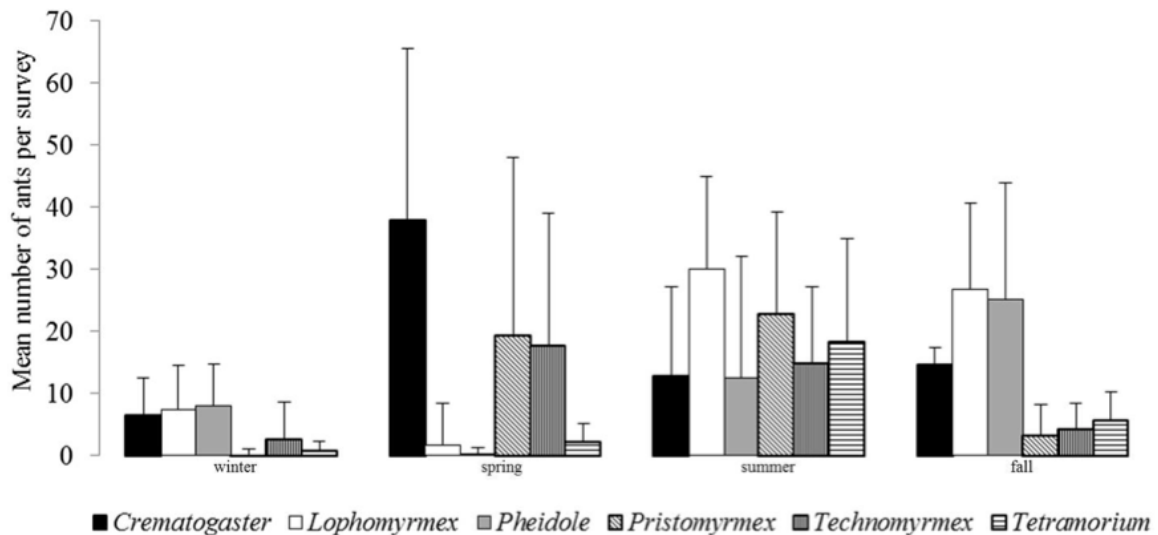


Fig. 4. Seasonal variations in the numbers of the six abundant ant species on male trees. All ant species showed significant differences among seasons (Kruskal–Wallis H test between seasons, all $P_s < 0.001$).

Fig-related factors

Among the three biotic factors (tree sex, fig abundance, and developmental phase), we found that ant abundance was significantly greater on male trees (mean \pm 1se: 4.44 ± 0.30 individuals per survey per tree) than on female trees (1.80 ± 0.29 individuals per survey per tree) (Mann–Whitney U test, $P < 0.001$). Ant abundance was also significantly correlated with the total number of figs (Pearson correlation coefficient: $R = 0.301$, $P < 0.001$) (Fig. 2), with more ants observed on trunks bearing figs (4.81 ± 0.35 individuals per survey per tree) than on trunks without figs (1.84 ± 0.21 individuals per survey per tree) (Mann–Whitney U test, $P < 0.001$). In addition, the resources provided by figs to ants varied with tree sex and fig developmental phase (Table 2). In terms of temporal sequence, the stalks of

A-phase figs were commonly colonized by aphids in both sexes, followed by the appearance of pollinating fig wasps (*Ceratosolen wui*) in B-phase figs for pollination and oviposition, and subsequent aggregation of *Philotrypesis* sp, the NPFW associated with *F. benguetensis*, only in male C-phase figs, and the final massive emergence of wasps from the D-phase figs on male trees. On female trees, flies (Psychodidae and Drosophilidae) were then attracted by the softened E-phase figs (Table 2).

The specific association between ant species and fig abundance varied not only with ant species, but also with fig sexes and maturity. Among the six most common ant species, we found that the abundance of *Lophomyrmex taivanae* and *Tetramorium nipponense* were significantly correlated with the number of male

**Table 2:** Correlation tests between the numbers of six abundant ant species and figs (either the total number of figs or in groups of figs of different sex and developmental phases that provide various food resources). The numbers in parenthesis were sample size for each correlation.

Phase	Resources for ants	<i>L. taivanae</i>	<i>C. s. formosae</i>	<i>Ph. n. noda</i>	<i>Pr. punctatus</i>	<i>Tet. nipponense</i>	<i>Tec.a. brunneus</i>
Total figs (1734)		0.35***	NS	NS	NS	0.30***	NS
All male figs (1122)		0.35***	NS	NS	NS	0.30***	NS
All female figs (612)		NS	NS	NS	NS	NS	NS
Grouping by fig phase							
Male A (179)	Hemipteran honeydew	0.36***	NS	NS	NS	NS	NS
Male B (39)	Pollinating fig wasp	NS	NS	NS	NS	NS	NS
Male C (378)	NPFW; Sugar	0.34***	NS	NS	NS	0.38***	NS
Male D (31)	Fig wasps	NS	NS	NS	NS	0.95***	NS
Female A (70)	Hemipteran honeydew	NS	NS	NS	NS	NS	NS
Female B (20)	Pollinating fig wasp	NS	NS	NS	NS	NS	NS
Female C (239)	None	NS	NS	NS	NS	0.27***	NS
Female E (12)	Seeds and fig flesh	NS	NS	NS	NS	NS	NS

Pearson correlation tests (with application of Bonferroni correction): *** $P < 0.001/66 = 1.52 \times 10^{-5}$; NS, not significant; NA, not applicable; NPFW, non-pollinating fig wasp.

figs. But the abundance of these two species was associated with different phases. *Lophomyrmex taivanae* ants associated with A- and C-phases while *Tetramorium nipponense* ants associated with C- and D-phases. These two species were both observed preying on wasps (Fig. 3C and 3D). None of the six abundant species was associated with total female figs, but the abundance of *Tetramorium nipponense* ants were correlated with the number of female C-phase figs (Table 2).

In addition to figs that served as food resources to the ant community, we observed that fig clusters on the trunk of *F. benguetensis* also provided nesting habitats for *Lophomyrmex* and *Crematogaster* ants (Fig. 3B).

DISSUSSIONS

To our knowledge, this is the first study that explores the effect of both abiotic and fig-related factors on the various ant communities occurring on *F. benguetensis*. With respect to abiotic factors, our results reveal that the composition and abundance of the ant communities exhibited significant seasonal variation, correlated specifically with temperature. In term of fig-related factors, the patterns of the ant communities were affected by tree sex, fig abundance, and developmental phases of the figs.

Dioecious *F. benguetensis* showed higher resource accessibility, diversity, and variability in male trees than female trees, resulting in higher species richness and abundance of ant communities on male *F. benguetensis*. Three characteristics of fig production could facilitate and complicate resource accessibility, e.g. phenology, fruiting locations, and forms of the fig crops. A significant sexual difference in phenological patterns was shown existing between male and female *F. benguetensis* trees (Lin *et al.*, 2015). Male trees produce fig crops multiple times within a year, and mainly on the trunk and lower parts of the branches (that could be more easily accessed by terrestrial ants), while female trees produce only one crop a year and

the majority of figs on twigs (about 90%) during the growing season. In addition, the trunk figs grow in clusters, while twig figs grow in scattered forms. These characteristics of fig production can cause varying food accessibility for ants on trees of different sex, which may in turn influence the richness and abundance of ant communities (Wilkinson and Feener, 2010; Chen *et al.*, 2011).

Diversity and the nature of the resources may also influence the patterns of the ant community on fig trees of different sex. Wasps, which appeared only on male trees, are a staple food resource for ants (Schatz *et al.*, 2008; Bain *et al.*, 2014a). Compared to plant-derived carbohydrate-rich resources, such as seeds and honeydew, wasps are protein-rich resources, which are crucial to the growth of the nest of the ants (Feldhaar *et al.*, 2007). The higher diversity in resources provided by male *Ficus* may increase the richness of foraging ant species (Ribas *et al.*, 2003), as each species has different nutrient requirements and feeding preferences. For example, hemipteran-tending ants may prefer honeydew over crystallized sugars because of the difference in the provided nutrients (Fischer *et al.*, 2002, 2005).

Finally, resource variability as well as resource diversity could reduce potential interspecific competition and increase the richness and abundance of ant communities, as in the case of the temporal heterogeneity effect on species co-existing in a community (Dunn *et al.*, 2007). Besides the temporal and seasonal changes in fig resources, several phases were commonly observed at the same time (Lin *et al.*, 2015). As the phenology of figs shows a low synchrony on *F. benguetensis*, multiple ant species with different food preferences and feeding habits may take advantage of the most beneficial resources available (Di Giusto *et al.*, 2001; Lanan, 2014).

Our results also show that some ant species are highly associated with certain fig phases and this association may imply their feeding habits. Although most ants are omnivorous, the proportions of the vegetal



and animal components in their diet vary greatly (Mooney and Tillberg, 2005; Gibb and Cunningham, 2011). In this study, *Lophomyrmex* and *Tetramorium* ants were associated with male figs. During the process of fig development, the C-phase figs are the most susceptible to parasitism. During this period, NPFWs of *F. benguetensis* attempt oviposition from outside the figs through the fig wall and are thus susceptible to ant predation (Compton *et al.*, 2009). Ant patrolling could increase predation on NPFWs, thereby limiting the impact of non-pollinating wasps (Schatz *et al.*, 2006; Harrison, 2014). In addition, the massive emergence of wasps from D-phase figs provides *Tetramorium* ants with wasp predation opportunities. Smallest in body size among the abundant ants, *Tetramorium* ants are also able to enter D-phase figs and consume the wingless agaonid male wasps trapped inside (S.-Y. Lin pers. obs.). Other ant species must chew a larger entrance for themselves long after all the winged female wasps have departed (A. Bain pers. obs.). Our study shows an unexpected result concerning *Crematogaster*, *Technomyrmex*, and *Pheidole* ants, all of them were common hemipteran-tending ants in early fig phases (A- and B-phases), but their occurrence exhibited no significant correlation with fig developmental phases. This could be attributed to the seasonality of their foraging. The abundance of these three ant species on the fig clusters on trunks was highly seasonal (e.g., *Crematogaster* and *Technomyrmex* ants were more active and abundant in spring and summer, while *Pheidole* ants, in fall). Such seasonality might have masked deeper relationships, at least with A-phase figs. Furthermore, *Tetramorium* ants were the only one species associated with female C-phase figs, but there is still uncertainty about which of the different resources provided by the figs attract them. Further investigation, including stable isotope analyses, is necessary to clarify the trophic status of all these species.

Beyond the fig-related factors, among the abiotic factors, temperature was observed exerting a particular influence on the occurrence of ant species on *F. benguetensis*. As the fig phenology of *F. benguetensis* is not correlated with either temperature or rainfall (Lin *et al.*, 2015), climate (temperature and rainfall) and fig-related factors (tree sex, fig abundance, and developmental phase) can be considered as two independent sets of variables affecting the composition and abundance of ant communities. Consistent with previous observations (Challet *et al.*, 2005; Lessard *et al.*, 2009; Pelini *et al.*, 2011), the abundance of ants in our study also showed positive correlation with temperature. The seasonal variation in composition and abundance of ant communities may result from the difference in temperature tolerance of each ant species (Cerdá *et al.*, 1998; Wittman *et al.*, 2010; Warren *et al.*, 2011). For example, *Crematogaster* and *Technomyrmex* ants were more active in spring and summer, while *Pheidole* ants,

in fall. On the other hand, there was no evidence indicating that the abundance of ants on *F. benguetensis* was correlated with rainfall. This could be explained by considering the climate of the native habitat of our study species. Given that *F. benguetensis* mainly grows in low-altitude environments with high humidity (Yang *et al.*, 2009), humidity brought about by rainfall should not be a limiting factor constraining the activities of foraging ants.

Besides dietary resource partitioning and seasonal variation of the foraging ant communities, we also observed an additional divergence in habitat utilization by ants as nesting sites. Since *F. benguetensis* is a tree of medium height, figs in clusters on the trunks of male trees attract both arboreal and terrestrial ants. Among the six abundant ant species, *Crematogaster*, *Lophomyrmex*, *Technomyrmex*, and *Tetramorium* are arboreal species (Brown and Gordon, 2000; Yusah *et al.*, 2011; Bain *et al.*, 2012), and *Pheidole* and *Pristomyrmex* ants are terrestrial species (Brown and Gordon, 2000; Satow *et al.*, 2013). Specifically we observed that *Crematogaster* and *Lophomyrmex* ants built their nests directly within the fig clusters (Fig. 3B). As a result, ant patrolling could take place more frequently on the trunk than on terminal branches, thereby limiting the impact of non-pollinating wasps (Schatz *et al.*, 2006; Harrison, 2014). This feature of *F. benguetensis* trees (cauliflory in male trees) may have evolved to diminish parasitism pressure. Considering that the fig-fig wasp mutualism has persisted for more than 60 million years (Rønsted *et al.*, 2005), and that ants are abundant on fig trees (Bain *et al.*, 2014a), it is reasonable to expect that ants may play a role as non-obligate mutualistic partners in the fig-fig wasp mutualism.

In conclusion, we have explored the extent to which two selected sets of abiotic and biotic factors influenced the diversity and abundance of the ant community occurring on *F. benguetensis* trees. This is the first study offering evidence of the bottom-up effect that linked resource diversification associated with figs of different sex and developmental phases to the complex ant community on dioecious *Ficus*. We suggest that dietary resource partitioning and temperature may be the main driving forces shaping the species composition of ant communities on *F. benguetensis*. Further studies on interspecific interactions as well as spatial distribution of ant communities among trees of *Ficus* are required to identify other contributing mechanisms for community structuring patterns.

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LITERATURE CITED

- Anderson, A. N.** 1997. Using ants as bioindicators: Multiscale issues in ant community ecology. *Conse. Ecol.* **1**(1): 8.
- Azcárate, F. M., E. Kovacs and B. Peco.** 2007. Microclimatic conditions regulate surface activity in harvester ants *Messor barbarus*. *J. Insect Behav.* **20**(3): 315–329.
- Bain, A., B. Chantarasuwan, M. Hossaert-McKey, B. Schatz, F. Kjellberg and L.-S. Chou.** 2012. A new case of ants nesting within branches of a fig tree: The case of *Ficus subpisocarpa* in Taiwan. *Sociobiol.* **59**: 415–434.
- Bain, A., L.-S. Chou, H.-Y. Tzeng, Y.-C. Ho, Y.-P. Chiang, W.-H. Chen, F. Kjellberg.** 2014b. Plasticity and diversity of the phenology of dioecious *Ficus* species in Taiwan. *Acta Oecol.* **57**: 124–134.
- Bain, A., R. D. Harrison and B. Schatz.** 2014a. How to be an ant on figs. *Acta Oecol.* **57**: 97–108.
- Bain, A., H.-Y. Tzeng, W.-J. Wu and L.-S. Chou.** 2015. *Ficus* (Moraceae) and fig wasps (Hymenoptera: Chalcidoidea) in Taiwan. *Bot. Stud.* **56**: 11.
- Berg, C. C.** 2011. Corrective notes on the Malesian members of the genus *Ficus* (moraceae). *Blumea – Biodiv. Evol. Biogeogr. Pl.* **56**: 161–164.
- Berg, C. C. and E. J. H. Corner.** 2005. Moraceae (*Ficus*). In: *Nooteboom, H. P.* (ed.), *Flora Malesiana*, Vol. 17. National Herbarium Nederland, Leiden.
- Blüthgen, N. and N. E. Stork.** 2007. Ant mosaics in a tropical rainforest in Australia and elsewhere: A critical review. *Austral Ecol.* **32**: 93–104.
- Blüthgen, N., N. E. Stork and K. Fiedler.** 2004. Bottom-up control and co-occurrence in complex communities: Honeydew and nectar determine a rainforest ant mosaic. *Oikos* **106**: 344–358.
- Bolton, B.** 1994. Identification guide to the ant genera of the world. Harvard University Press, Cambridge, USA.
- Brown, M. J. F. and D. M. Gordon.** 2000. How resources and encounters affect the distribution of foraging activity in a seed-harvesting ant. *Behav. Ecol. Sociobiol.* **47**(3): 195–203.
- Cerdá, X., J. Retana, and S. Cros.** 1998. Critical thermal limits in mediterranean ant species: trade-off between mortality risk and foraging performance. *Funct. Ecol.* **12**(1): 45–55.
- Challet, M., C. Jost, A. Grimal, J. Lluc, and G. Theraulaz.** 2005. How temperature influences displacements and corpse aggregation behaviors in the ant *Messor sancta*. *Insectes Sociaux.* **52**(4): 309–315.
- Chen, Y., S. Wang and Z. Lu.** 2011. Foraging strategies may mediate the coexistence of ant species attending *Kerria yunnanensis* on their host plant. *Bull. of Insectol.* **64**(2): 181–188.
- Chen, C.-H. and L.-Y. Chou.** 1997. The Blastophagini of Taiwan (hymenoptera: Agaonidae: Agaoninae). *J. Taiwan Mus.* **50**: 113–154.
- Compton, S. G. and H. G. Robertson.** 1991. Effects of ant-homopteran systems on fig-fig wasp interactions. In: *Huxley, C. R. and D. F. Cutler* (eds.), *Ant-plant interactions*, Oxford University Press, Oxford. pp. 120–130.
- Compton, S. G., S. van Noort, M. McLeish, M. Deeble and V. Stone.** 2009. Sneaky African fig wasps that oviposit through holes drilled by other species. *Af. Nat. Hist.* **5**: 9–15.
- Davidson, D. W.** 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biol. J. Linn. Soc.* **61**(2): 153–181.
- Davidson, D. W. and L. Pattrel-Kim.** 1996. Tropical arboreal ants: Why so abundant? In: *Gibson, A. C.* (ed.), *Neotropical biodiversity and conservation*. University of California, Los Angeles. pp. 127–140.
- Davidson, D. W., S. C. Cook, R. R. Snelling and T. H. Chua.** 2003. Explaining the abundance of ants in lowland tropical rainforest canopies. *Science* **300**: 969–972.
- Dejean, A., B. L. Fisher, B. Corbara, R. Rarevohitra, R. Randrianaivo, B. Rajemison and M. Leponce.** 2010. Spatial distribution of dominant arboreal ants in a Malagasy coastal rainforest: Gaps and presence of an invasive species. *PLoS ONE* **5**: e9319.
- Di Giusto, B., M.-C. Anstett, E. Dounias and D. B. McKey.** 2001. Variation in the effectiveness of biotic defence: The case of an opportunistic ant-plant protection mutualism. *Oecologia* **129**: 367–375.
- Dunn, R. R., C. R. Parker and N. J. Sanders.** 2007. Temporal patterns of diversity: assessing the biotic and abiotic controls on ant assemblages. *Biol. J. Linn. Soc.* **91**(2): 191–201.
- Feldhaar, H., J. Straka, M. Krischke, K. Berthold, S. Stoll, M. J. Mueller and R. Gross.** 2007. Nutritional upgrading for omnivorous carpenter ants by the endosymbiont *Blochmannia*. *BMC Biol.* **5**: 48.
- Fischer, M. K., W. Völkl and K. H. Hoffmann.** 2005. Honeydew production and honeydew sugar composition of polyphagous black bean aphid, *Aphis fabae* (Hemiptera: Aphididae) on various host plants and implications for ant-attendance. *Eur. J. Entomol.* **102**(2): 155–160.
- Fischer, M. K., W. Völkl, R. Schopf and K. H. Hoffmann.** 2002. Age-specific patterns in honeydew production and honeydew composition in the aphid *Metopeurum fuscoviride*: Implications for ant-attendance. *J. Ins. Physiol.* **48**: 319–326.
- Galil, J. and D. Eisikowitch.** 1969. Further studies of the pollination ecology of *Ficus sycomorus* L. (Hymenoptera, Chalcidoidea, Agaonidae) *Tijdschrift v. Entomol.* **112**(3): 1–13.
- Gordon, D. M., K. N. Dektar and N. Pinter-Wollman.** 2013. Harvester ant colony variation in foraging activity and response to humidity. *PLoS ONE.* **8**(5): e63363.
- Gibb, H. and S. A. Cunningham.** 2011. Habitat contrasts reveal a shift in the trophic position of ant assemblages. *J. Anim. Ecol.* **80**(1): 119–127.
- Harrison, R. D.** 2014. Ecology of a fig ant-plant. *Acta Oecol.* **57**: 88–96.
- Heil, M., J. Rattke, and W. Boland.** 2005. Postsecretory hydrolysis of nectar sucrose and specialization in ant/plant mutualism. *Science* **308**(5721): 560–563.
- Hunter, M. D.** 2009. Trophic promiscuity, intraguild predation and the problem of omnivores. *Agr. Forest Entomol.* **11**(2): 125–131.
- Kerdelhué, C. and J.-Y. Rasplus.** 1996. Non-pollinating Afrotropical fig wasps affect the fig-pollinator mutualism in *Ficus* within the subgenus *Sycomorus*. *Oikos* **75**: 3–14.
- Kuaraksa, C., S. Elliott and M. Hossaert-McKey.** 2012. The phenology of dioecious *Ficus* spp. Tree species and its importance for forest restoration projects. *For. Ecol. Manag.* **265**: 82–93.



- Lanan, M.** 2014. Spatiotemporal resource distribution and foraging strategies of ants (Hymenoptera: Formicidae). *Myrmecol. News* **20**: 53–70.
- Lessard, J. P., R. R. Dunn, N. J. Sanders.** 2009. Temperature-mediated coexistence in temperate forest ant communities. *Insectes Sociaux* **56**(2): 149–156.
- Lin, S.-Y., L.-S. Chou, B. Di Giusto and A. Bain.** 2015. Sexual specialization in phenology in dioecious *Ficus benguetensis* and its consequences for the mutualism. *Bot. Stud.* **56**: 32.
- Lin, C.-C. and W.-J. Wu.** 2003. The ant fauna of Taiwan (Hymenoptera: Formicidae), with the keys to subfamilies and genera. *Ann. Nat. Taiwan Mus.* **45**: 5–69.
- Martínez-Mota, R., J. C. Serio-Silva and V. Rico-Gray.** 2004. The role of canopy ants in removing *Ficus perforata* seeds from howler monkey (*Alouatta palliata mexicana*) feces at Los Tuxtlas, México. *Biotropica* **36**: 429–432.
- Maschwitz, U., B. Fiala, L. G. Saw, N.-R. Yusoff and A. H. Idris.** 1994. *Ficus obscura* var. *Borneensis* (Moraceae), a new non-specific ant-plant from Malesia. *Mal. Nat. J.* **47**(4): 409–416.
- Mooney, K. A. and C. V. Tillberg.** 2005. Temporal and spatial variation to ant omnivory in pine forests. *Ecology* **86**: 1225–1235.
- Novotny, V., Y. Basset, J. Auga, W. Boen, C. Dal, P. Drozd, K. Molem.** 1999. Predation risk for herbivorous insects on tropical vegetation: A search for enemy-free space and time. *Austral. J. Ecol.* **24**(5): 477–483.
- Pelini, S. L., M. Boudreau, N. McCoy, A. M. Ellison, N. J. Gotelli, N. J. Sanders, R. R. Dunn.** 2011. Effects of short-term warming on low and high latitude forest ant communities. *Ecosphere* **2**(5): art62.
- Patel, A., M. C. Anstett, M. Hossaert-McKey and F. Kjellberg.** 1995. Pollinators entering female dioecious figs: why commit suicide? *J. Evolution Biol.* **8**(3): 301–313.
- Ribas, C. R., J. H. Schoederer, M. Pic and S. M. Soares.** 2003. Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. *Austral. J. Ecol.* **28**(3): 305–314.
- Roberts, J. T. and E. R. Heithaus.** 1986. Ants rearrange the vertebrate-generated seed shadow of a neotropical fig tree. *Ecology* **67**: 1046–1051.
- Roces, F. and C. Kleineidam.** 2000. Humidity preference for fungus culturing by workers of the leaf-cutting ant *Atta sexdens rubropilosa*. *Insectes Sociaux* **47**(4): 348–350.
- Rønsted, N., G. D. Weiblen, J. M. Cook, N. Salamin, C. A. Machado and V. Savolainen.** 2005. 60 million years of co-divergence in the fig–wasp symbiosis. *Proc. Roy. Soc. B* **272**: 2593–2599.
- Sanders, N. J., G. M. Crutsinger, R. R. Dunn, J. D. Majer and J. H. C. Delabie.** 2007. An ant mosaic revisited: Dominant ant species disassemble arboreal ant communities but co-occur randomly. *Biotropica* **39**: 422–427.
- Satow, S., T. Satoh and T. Hirota.** 2013. Colony fusion in a parthenogenetic ant, *Pristomyrmex punctatus*. *J. Ins. Sci.* **13**: 1–16.
- Schatz, B. and M. Hossaert-McKey.** 2003. Interactions of the ant *Crematogaster scutellaris* with the fig/fig wasp mutualism. *Ecol. Entomol.* **28**: 359–368.
- Schatz, B., F. Kjellberg, S. Nyawa and M. Hossaert-McKey.** 2008. Fig wasps: A staple food for ants on *Ficus*. *Biotropica* **40**: 190–195.
- Schatz, B., M. Proffit, B. V. Rakhi, R. M. Borges and M. Hossaert-McKey.** 2006. Complex interactions on fig trees: Ants capturing parasitic wasps as possible indirect mutualists of the fig-fig wasp interaction. *Oikos* **113**(2): 344–352.
- Shanahan, M., S. So, S. G. Compton and R. T. Corlett.** 2001. Fig-eating by vertebrate frugivores : A global review. *Biol. Rev.* **76**: 529–572.
- Terayama, M.** 2009. A synopsis of the family Formicidae in Taiwan (Insecta, Hymenoptera). *Bull. Kanto Gakuen Univ.* **17**: 81–266.
- Warren, R. J. I., V. Bahn and M. A. Bradford.** 2011. Temperature cues phenological synchrony in ant-mediated seed dispersal. *Global Change Biol.* **17**: 2444–2454.
- Wilkinson, E. B. and D. H. Feener.** 2010. Variation in resource size distribution around colonies changes ant–parasitoid interactions. *Insectes Sociaux* **57**(4): 385–391.
- Wilson, E. O. and B. Hölldobler.** 2005. The rise of the ants: A phylogenetic and ecological explanation. *Proc. Nat. Acad. Sci. USA* **105**: 7411–7414.
- Wittman, S. E., N. J. Sanders, A. M. Ellison, E. S. Jules, J. S. Ratchford, N. J. Gotelli.** 2010. Species interactions and thermal constraints on ant community structure. *Oikos* **119**(3): 551–559.
- Yang, D.-L., H.-Y. Tzeng, K.-Y. Su, N.-L. Zu, K.-S. Lai and Y.-H. Tseng.** 2009. Study on the Vegetation of Toului Submontane Area. *Quart. J. of For. Res.* **31**(3): 17–33.
- Yusah, K. M., T. M. Fayle, G. Harris and W. A. Foster.** 2011. Optimizing diversity assessment protocols for high canopy ants in tropical rain forest. *Biotropica* **44**: 73–81.