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Disturbance effects on community structure of *Ficus tinctoria* fig wasps in Xishuangbanna, China: Implications for the fig/fig wasp mutualism

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Abstract Fig trees are important components of tropical forests, because their fruits are eaten by so many vertebrates, but they depend on pollinating fig wasps to produce mature fruits. Disturbance to habitat structure can have a major impact on insect diversity and composition, potentially reducing fruit yields. We investigated the impact of habitat disturbance on the fig wasp community associated with male figs of *Ficus tinctoria* in Xishuangbanna, China. The community comprised one pollinator species *Liporrhopalum gibbosae* and six non-pollinating wasp species: *Sycoscapter* sp.1, *Philotrypesis ravii*, *Philotrypesis* sp.1, *Neosycophila omeomorpha*, *Sycophila* sp.1, and *Walkerella* sp.1. More disturbed areas were characterized by higher temperatures, less shade, and more vehicle noise. The response of the fig wasp community was complex, with no simple relationship between intensity of disturbance and pollinator abundance. However, the sex ratios (proportion of male progeny) of pollinators increased significantly in more disturbed areas. We conclude that potential changes in fig wasp community composition brought about by disturbance, are unpredictable, with unclear consequences for tropical rainforest biodiversity.

Key words disturbance, *Ficus tinctoria*, fig/fig wasp mutualism, wasp community

Introduction

The responses of individual species to disturbance are highly variable (Niemela *et al*., 2000). In disturbed habitats, remnant vegetation is typically altered in structure and composition and often supports communities dominated by non-native flora and fauna (Beissenger & Osborne, 1982; Blair, 1996; Marzluff & Ewing, 2001; King & Buckney, 2002). Habitat disturbance also affects faunal diversity and composition (Uetz, 1979; August, 1983). There is little information about the responses of mutualisms to habitat variation (Bronstein, 1989), and few studies of how fig wasp communities respond to disturbance (Wang *et al*., 2005).

There are approximately 750 tropical and extra-tropical fig species (*Ficus* spp., Moraceae) that are pollinated by highly specific chalcidoid wasps (Hymenoptera: Agaonidae) (Hawkins & Compton, 1992; Berg, 2003; Yu *et al*., 2008). These fig wasp species include both pollinators and non-pollinators (West *et al*., 1996). The mutualism is obligate, the fig pollen is dispersed only by the wasps, and they complete their life cycle inside the figs (Herre, 1989; West *et al*., 1996). Mated, pollen-bearing female pollinators enter figs (highly modified inflorescences), pollinate the tiny female flowers and oviposit in some of them (Galil & Eisikowitch, 1968; Herre, 1989, 1996). The wasps develop by consuming the contents of one ovule each. The young adults emerge, mate, gather pollen either actively or passively, leave the natal fig, and

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fly off to seek a receptive fig in which to begin a new cycle. The fig fruits ripen and are consumed by vertebrate frugivores and surviving seeds are dispersed (Kalko *et al.*, 1996; Shanahan *et al.*, 2001; Yu *et al.*, 2008).

There are many non-pollinating wasps that are apparently parasitic and provide no obvious benefit to the fig (West & Herre, 1994). Most of them insert their ovipositors through the fig wall and oviposit from outside (West & Herre, 1994; Yu *et al*., 2008). The competition for available female flower resources between pollinators and non-pollinators, as well as the parasitism of pollinators, reduces their numbers and may disrupt their mutualism with fig trees (West & Herre, 1994; Kerdelhué & Rusplus, 1996; Kerdelhué *et al*., 2000; Wang *et al*., 2005).

Environmental disturbance to forests, including road-building, clearance and other human activities, is increasing, and has had direct impact on native biodiversity (Norton & Miller, 2000). Comparisons of the structure of fig wasp communities in forests subject to varying levels of disturbance may improve our understanding of both the relationship between pollinating wasps and non-pollinating wasps and the impact of the non-pollinators on the mutualism between figs and their pollinating wasps (Wang *et al*., 2005). Wang *et al*. (2005), working with *Ficus racemosa* in south China, found that habitat disturbance resulted in a higher proportion of non-pollinating wasps compared with less fragmented forest. However, it is not clear how these changes are driven. Herre (1996) concluded that several physiological aspects of figs such as photosynthesis, temperature and water have certain influences on the wasp community.

In this study, we addressed the following questions. Are there significant differences between fig wasp community structures with increasing habitat disturbance? What are the implications of changes in wasp community structure on the interaction between the figs and their pollinating wasps?

Materials and methods

Sample sites

This study was carried out in the Xishuangbanna Tropical Botanical Garden, Yunnan, China, located at 21°41″N, 101°25″E, and an altitude of approximately 600 m. The climate is characterized by dry, rainy and foggy seasons, which last from March to May, June to October and November to February, respectively. The annual mean precipitation is 1 557 mm, approximately 79%–82% of which occurs during the rainy season. The average ambient relative humidity is 86% and the average temperature each year is 21.4–22.6°C. January is the coldest month (average temperature, 11.2°C), and April is the hottest (33.5°C) (Yang *et al*., 2000; Zhu & Cai, 2005; Wang *et al*., 2005).

Ficus tinctoria *and its fig wasps*

Ficus tinctoria Forst. f. (section *Sycidium*, subgenus *Sycidium*) is a strangling dioecious fig tree, which is distributed throughout much of Asia. The leaf blade is often asymmetric, and the margin is often dentate and sometimes lobed (Zhou & Gilbert, 2003). It produces very large numbers of relatively small-sized figs (11.40 ± 1.66 cm diameter when mature ($n = 122$). Fruit formation mostly occurs during the foggy and dry seasons (October–May). Fruit initiation on male trees peaks from October onward, with wasps being released after approximately 3 months. This coincides with numerous female crops, which ripen in a shorter time than those on male trees. Male figs contain about 200 female flowers, whereas female flower numbers in female figs is only about 140. Female crops are more synchronous than those on male trees.

Ficus tinctoria is pollinated by the fig wasp *Liporrhopalum gibbosae* Hill (Agaonidae, Chalcidoidea). Non-pollinator wasps recorded locally from the figs of *F. tinctoria* include *Sycoscapter* sp.1, *Philotrypesis ravii* and *Philotrypesis* sp.1, (Sycoryctinae, Pteromalidae), *Neosycophila omeomorpha* (Epichrysomallinae), *Sycophila* sp.1 (Eurytomidae), and *Walkerella* sp.1 (Otitesellinae, Pteromalidae). Females of all the non-pollinating wasp species oviposit from outside the figs, so they cannot contribute to pollination.

Fig wasp sampling

Between November 2007 and March 2008, eight crops were collected from eight different *F. tinctoria* trees growing in the Xishuangbanna Tropical Botanical Garden. The trees were chosen to represent sites with varying levels of local disturbance. The trees in the least disturbed area were growing in a shaded forest situation, surrounded by trees and shrubs, with some grasses. Alternatively, trees in the most disturbed areas were fully exposed to the sun, with almost no nearby vegetation and adjacent roads.

Thirty figs were collected at random from each tree. They were at the stage where male wasps had already started to emerge from the galls, but no wasps had vacated the figs. The figs were placed individually into muslin bags (20 cm × 15 cm), then sliced open to help the wasps to emerge before the bags were closed (Xu *et al*., 2002; Bai *et al*., 2006). The wasps from each fig were then stored in 75% ethanol. The wasps were subsequently examined under a stereomicroscope, identified, counted and sexed (Yu *et al*., 2008).

Environmental correlates

In order to characterize the environments where the trees were growing, we recorded relevant environmental conditions. On a sunny day in February (mean temperature $\approx 25°C$), we measured diurnal variation in photosynthesis of the fig leaves, air temperature and the ambient relative humidity (RH) using an Li-6400XT portable photosynthesis system (Li-cor, Lincoln, NE, USA). On seven trees we selected three attached leaves (the leaves had to be detached from Tree 2 because of accessibility problems) which were ≈ 1.5 m high from the ground and exposed to the sun. Recordings were taken every 3 h from 08:00 to 19:00 hours (Jin & Ke, 2004; Shao *et al.*, 2006). On another sunny day (mean temperature $\approx 20°C$), we measured soil moisture (weight of water/weight of water and dry soil) from the surface 0–30 cm deep, based on four scattered soil samples from each tree. Further, according to full, half, and no shade around the experiment trees, and also the number of buildings around them, as well as people and traffic across them, we also divided the shade and noise of the microenvironment of each tree into three levels.

Statistical analysis

Statistical analyses were performed with SPSS 16.0, Statgraphics software and Multivariate Statistical Package. Data were analyzed using Spearman's rank correlation, principle components, linear regression, and Mann–Whitney U-tests.

Results

The wasp community of F. tinctoria

A total of 39 204 fig wasps in 242 figs were collected from the eight trees of *Ficus tinctori* (Table 1). Seven species of fig wasps were recorded. The number of wasps in each fig tree varied from (mean ± SD) 117.4 ± 37.0 to 214.5 ± 56.1 with the pollinator the most abundant species (127.2 ± 65.5 individuals per fig), then *Sycoscapter* sp.1 (37.8 ± 28.5) and *Phylotrypesis* ravii (8.6 ± 7.4) (Fig. 1). There was a negative relationship between the numbers of pollinators and non-pollinating wasps in the figs (linear regression, $F = 27.88$, $P < 0.001$, Fig. 2)

Table 1 The abundance and frequency of occurrence of fig wasps recorded from eight *F. tinctoria* crops at Xishuangbanna Tropical Botanical Garden, Yunnan, China.

	Tree number							
	1	2	3	4	5	6	7	8
Sample size (figs)	29	30	30	30	31	31	30	30
Percentage of total wasps (No. figs present)								
Liporrhopalum gibbosae	54.08 (29)	80.5 (30)	97.04 (30)	86.9 (30)	86.96 (31)	64.48 (31)	64.48 (30)	82.49 (30)
Sycoscapter sp.1	44.34 (29)	19.29 (30)	2.55 (15)	13.1 (25)	12.18 (25)	34.42 (31)	31.28 (29)	15.46 (30)
Philotrypesis ravii	1.51 (8)	0.21 (1)	0.42 (6)	0 (0)	0.84 (7)	1.07 (10)	4.23 (13)	2.06 (12)
Philotrypesis sp.1	0 (0)	0 (0)	0 (0)	0 (0)	0.02 (1)	0 (0)	0 (0)	0 (0)
Neosycophila omeomorpha	0.04 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Sycophila sp.1	0.02 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0.03 (1)	0 (0)	0 (0)
Walkerella sp.1	0.02 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Total wasps (mean ± SD)	173.8 ± 52.1	143.7 ± 51.9	159.7 ± 37.5	165.4 ± 57.7	214.5 ± 56.1	117.4 ± 37.0	133.8 ± 65.5	193.0 ± 39.5

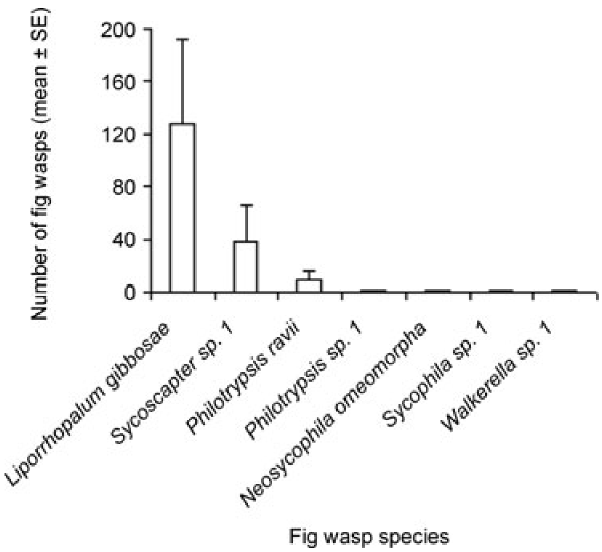

Fig. 1 The relative abundance of fig wasp species in male figs of *F. tinctoria*. Totals are based on crops from eight trees.

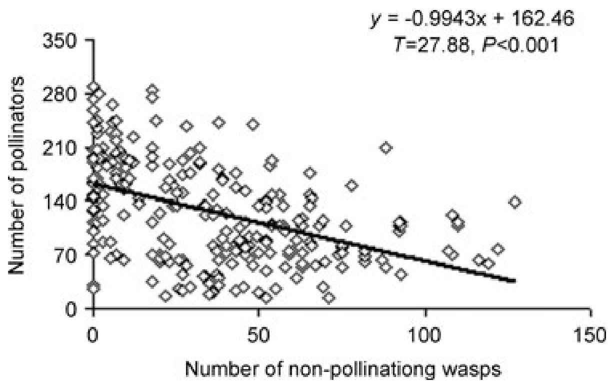

Fig. 2 The relationship between the numbers of non-pollinator and pollinator fig wasps in *F. tinctoria* figs.

Influences of disturbance on fig wasp community

The principle components analysis (pca) included physiological and climatic factors (photosynthesis, air temperature, ambient RH, soil moisture, shade and noise [Table 2, Fig. 3]). The first axis of the pca corresponds to variation in the disturbance at each site and provides a relative disturbance ranking for the eight trees (Fig. 3). With increasing disturbance, as measured by pca axis 1, the sex ratio (proportion of male progeny) of pollinators increased significantly with increasing levels of disturbance (linear regression, $P < 0.01$, Fig. 4). We also used the Mann–Whitney U-test, but there was no simple relationship between intensity of disturbance and pollinator

Table 2 The values for disturbance, microclimate and physiological factors for each *F. tinctoria* fig tree.

Tree no.	1	2	3	4	5	6	7	8
Photosynthesis (μmol$CO_2 \cdot m^{-2} \cdot s^{-2}$)	0.27 ± 0.65	0.57 ± 0.47	0.17 ± 0.11	2.23 ± 0.13	3.80 ± 0.35	3.07 ± 0.80	0.55 ± 0.05	2.14 ± 1.64
Air temperature (°C)	26.23 ± 0.14	25.64 ± 0.36	25.48 ± 0.47	25.29 ± 0.27	27.00 ± 0.58	28.18 ± 0.42	24.63 ± 0.15	25.56 ± 0.18
Ambient relative humidity (RH) (%)	51.83 ± 0.46	51.93 ± 0.58	52.90 ± 1.10	55.67 ± 0.79	56.53 ± 0.30	54.35 ± 0.50	56.95 ± 0.43	57.52 ± 2.33
Soil moisture (%)	10.08 ± 1.22	10.40 ± 0.62	11.01 ± 1.39	16.80 ± 1.30	13.13 ± 1.52	13.48 ± 1.67	12.21 ± 0.95	13.03 ± 1.45
Shade level (1–3, low–high)	2	3	3	2	1	1	2	2
Noise level (1–3, low–high)	3	1	1	3	2	2	2	2

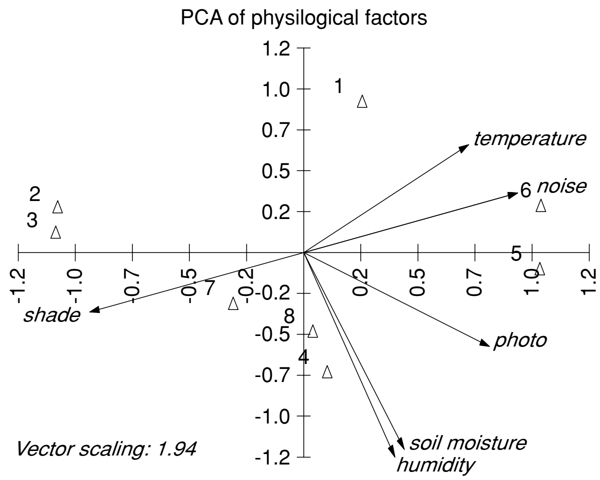

Fig. 3 Principle components analysis of environmental conditions around eight *F. tinctoria* trees. Axis one reflects a gradation in local habitat disturbance.

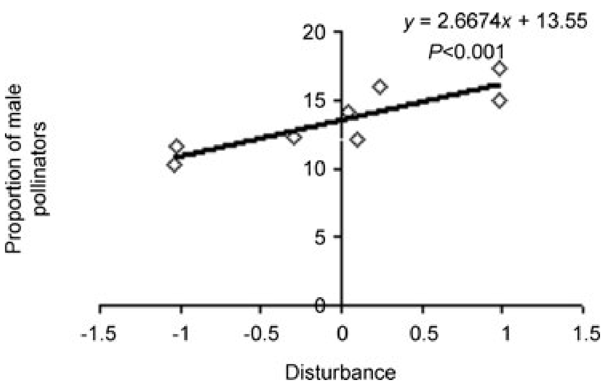

Fig. 4 The variation of sex ratio of pollinator at different levels of disturbance.

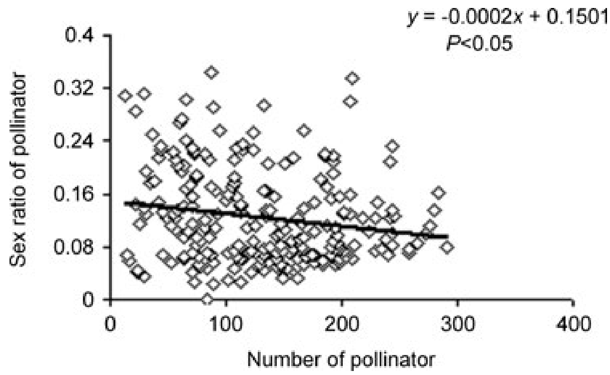

Fig. 5 The relationship between the number of pollinator and sex ratio of pollinators per fig.

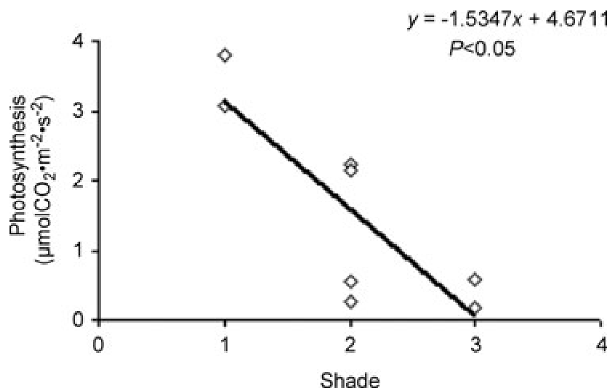

Fig. 6 The relationship between the environment factors shade and photosynthesis.

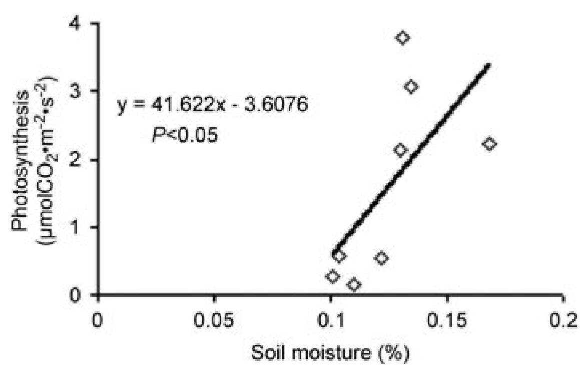

Fig. 7 The relationship between the environment factors soil moisture and photosynthesis.

abundance influenced by each environmental factor. Also, with the increasing numbers of pollinators, the sex ratio of pollinators decreased slightly (linear regression, $P < 0.05$, Fig. 5), but there was no significant relationship between the number of total wasps and the sex ratio of pollinators per fig. Pairing the environmental variables against each other in turn, we found that there was a significant negative relationship between shade and photosynthesis (linear regression, Fig. 6; Spearman's rank correlation, $P < 0.05$) and a positive relationship between soil moisture and photosynthesis (linear regression, Fig. 7; Spearman's rank correlation, $P < 0.05$). Others against each other were not strongly related.

Discussion

The wasp community associated with F. tinctoria *figs*

The data show that the wasp community of *Ficus tinctoria* included one pollinator and six non-pollinating wasp species. Among the non-pollinating species, two (*Sycoscapter* sp.1 and *Philotrypesis ravii*) were common and the other four species were rare. There was a negative relationship between the number of pollinators and non-pollinating wasps. Better understanding of the effects of these parasitic wasps on the fig/fig wasp mutualism requires knowledge of their larval diets. Observations showed that the *Sycoscapter* sp.1 wasps may be direct parasitoids of the pollinators. This non-pollinator was observed to oviposit from outside the fig wall in the D-phase, when there were no appropriate female flowers to occupy, but only galls (by author observation). *Philotrypesis ravii* is another common non-pollinating fig wasp parasite on *Ficus tinctoria.* Its success in exploiting the fig-pollinator mutualism may be explained by the fact that these parasites are apparently using the same pool of flowers as the pollinators. The parasitic wasps exploit flowers in which the pollinators grow and in which the fig apparently cannot differentiate between a parasite and a pollinator.

Disturbance influences on fig wasp community

Habitat structure and disturbance may broadly affect faunal diversity and composition in terrestrial systems (Uetz, 1979; August, 1983; Humphrey *et al*., 1999; Hansen, 2000; Lassau & Hochuli, 2004). This study is one of the few studies combining the factors of plant physiology to rank the disturbance of the site where the fig trees grow. We found with the increasing level of disturbance characterized by higher temperature, less shade and heavier noises, the response of the fig wasp community was complex, with no simple relationship between intensity of disturbance and pollinator abundance. This is different from the findings by Wang *et al.* (2005) that higher proportion of pollinators was found in more fragmented forest. The complicated relationship of the environmental factors between each other is an important reason for these results. The results and the interpretations presented here should properly be considered preliminary and tentative, requiring further substantiation.

Sex ratio of pollinators was affected by disturbance. In many organisms mating takes place between the offspring of one or a few foundress mothers in isolated subpopulations from which mated females disperse to found new broods. Under these conditions, local mate competition (LMC) should select for female-biased sex ratios (Hamilton, 1967; Herre, 1985). With increasing disturbance, the sex ratio of pollinators significantly increased. Also, the number of pollinators had negative effects on the sex ratio of pollinators. Thus, in most disturbed areas, with fewer pollinators there was a higher proportion of males. This is what would be predicted on the basis of figs with fewer pollinators being entered by more foundresses – they lay more eggs and a higher proportion of those eggs are male. Meanwhile, the total number of wasps had no significant influence on the pollinator sex ratio. If we assume that each non-pollinator developed at the expense of one pollinator, this then gives us information that non-pollinators altered the sex ratio. In most disturbed areas, the temperature and photosynthesis were higher, so the density of figs was higher and this provides more chances for foundresses to re-enter the second and third figs. Thus, they produce more males in the second or third figs (Raja *et al.*, 2008).

In southeast Asia and the neotropics, figs are viewed as a keystone plant resource; they support a wide spectrum of vertebrate frugivores during periods of food scarcity (Krebs, 1978; Thornton *et al.*, 1996; Nason *et al.*, 1998; Harrison, 2003; Wang *et al.*, 2005). Their importance in the conservation of many tropical forest communities is becoming increasingly recognized (McKey, 1989; Herre, 1996). Thus the stability of interactions in remaining rainforest fragments is an issue of considerable concern for conservation (Harrison, 2003). However, until now disturbance affects on fig wasp communities are not clear and cannot be predicted, and this requires scientists in related fields to undertake further and deeper research on the subject.

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