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The community structure of insects associated with figs at Xishuangbanna, China

Da-Rong Yang[1*], Yan-Qiong Peng[1], Pei Yang[1,2], and Jun-Ming Guan[1,2]

[1]Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming, Yunnan 650223, China, Tel. +86-871-512-7180, Fax. +86-871-516-0916, Email. yangdr@xtbg.ac.cn;
[2]Graduate University of Chinese Academy of Sciences, Beijing 100049, China

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Abstract

Ficus racemosa, *Ficus benjamina*, *Ficus auriculata* and *Ficus hispida* are the most common fig species in primary and secondary forests at Xishuangbanna. Several different insect functional groups that utilize these figs can be recognized: pollinating fig wasps; non-pollinating fig wasps including gall-makers, parasites and inquilines; pulp eating insects; insect predators; sap feeding insects; and decomposers. We studied the structure of these insect communities on each of the four common fig species. Of 116,719 insects collected, six orders, 23 families, 40 genera, and 65 species were identified. Pollinators comprised the fewest species, but the largest number of individuals. There was an abundance of non-pollinators on monoecious figs (*F. racemosa* and *F. benjamina*). In dioecious figs, male figs harbored more non-pollinators, but female figs attracted more pulp eating insects. The position and size of inflorescences on the different fig species were important traits in determining the associated insect communities. Cauliflorous species of fig (those bearing figs on trunks and branches, rather than on the ends of twigs), and those with larger fruits, supported both individually abundant, and species-rich, insect communities. Both diversity and evenness of insect communities were higher in primary rainforest, as compared with secondary forest. Thus, fig-associated insect communities may be used as indicators of forest quality, for the purposes of the protection and restoration of tropical rainforest.

Keywords: Fig trees, fig wasps, sap feeding insects, predators, decomposers, insect community, community structure

1. Introduction

Xishuangbanna has the largest area of tropical rainforest in China, and *Ficus* spp are an important component of these forests. The fig, a closed urn-shaped inflorescence, is the defining feature of *Ficus* (Moraceae), with approximately 750 species distributed pan-tropically. There are 97 species and more than 50 varieties in China, with 49 species and 23 varieties being recorded in the tropical areas of Xishuangbanna (Berg, 1989; Wu, 1995).

Fig species and their fig-pollinating wasps comprise a highly specific obligate mutualism. Fig trees depend on fig wasps to pollinate them and fig wasps reproduce only in the ovaries of their host figs. It is one of the most intricately co-evolved plant-insect interactions known (Ramirez, 1970; Wiebes, 1979; Weiblen, 2002). Most fig species also harbor non-pollinating wasps, including gallers, inquilines and parasitoids, and other insects such as pulp eating insects, sap feeding insects, insect predators and decomposers (West et al., 1996; Kerdelhué and Rasplus, 1996). The pollinating and non-pollinating wasps develop in galled ovules, while other insect groups usually live in the fig wall or on the outside of the fig. Many insects directly influence the development of the inflorescence, and thus seed and pollinator production. Fig trees bear fruits year-round in tropical rainforests, and hence are often considered to be keystone plants.

Ficus racemosa, *F. benjamina*, *F. auriculata* and *F. hispida* are the most common fig species in the primary and secondary forests at Xishuangbanna. The structure of insect communities and their functional groups on fig inflorescences have been little studied (Yang et al., 1997; Peng et al., 2002, 2003; Xu et al., 2003), but warrant attention as a result of their potential to affect fig and fig pollinator reproductive success. Hence, we investigated the insect communities and the ecological characteristics of different insect functional groups on four common fig species in Xishuangbanna tropical rainforest.

The author to whom correspondence should be sent.

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2. Study Sites, Materials and Methods

Sites

Three sampling sites were selected on basis of the distribution of fig trees and the degree of human disturbance. (i) Menglun primary rainforest: The area is 86000 ha., and is the core area of the Menglun Nature Reserve. The tropical rainforest is generally well conserved with 95% of the area covered by forests, but slightly disturbed by people and livestock. (ii) Xishuangbanna Tropical Botanical Garden comprised of secondary forest 3.5 ha in extent, which has been increasingly disturbed by local people in recent years. (iii) Ravine rainforest, comprised of 90 ha. of mixed primary forest and good quality secondary forests.

Materials

Ficus racemosa (section *Sycomorus*) is a monoecious species distributed along rivers and in gullies. Figs of the male floral phase measure 32.89 mm (s.d 4.59, n=117) in diameter, and figs are borne on the trunk and larger branches. The trees bear figs 1–6 times per year, asynchronously, at the population-level.

Ficus benjamina (section *Conosycea*) is a monoecious hemi-epiphyte found in secondary forests, and planted along streets and in gardens. Figs of the male floral phase are 20.67 mm (s.d 2.01, n=40) in diameter on average and borne in the leaf axils. The trees bear figs twice per year, in synchronous crops that are asynchronous at the population-level.

Ficus auriculata (section *Neomorphe*) is a dioecious tree that grows in both primary and secondary forests. Figs of the male floral phase are very large (66.69 mm s.d 9.21, n=40) and cauliflorous. Most of female trees have figs year-round with two peaks in production. Male trees bear figs in asynchoronous crops three times per year.

Ficus hispida (section *Sycocarpus*) is a dioecious fig tree that is found in wasteland and secondary forests, and is a common pioneer tree species. The figs of the male floral phase are smaller (29.82 cm s.d 5.86, n=40) and are cauliflorous, or on long runners growing down from the branches or trunk. Figs are produced by both sexes in moderate numbers year-round.

Table 1. The communities of fig wasps collected from four species of figs at Xishuangbanna, China.

Ficus species	Families/sub-families of fig wasps	Species of fig wasps	Biology
Ficus racemosa	Agaonidae	*Ceratosolen fusciceps*	Pollinators
	Sycophaginae	*Apocryptophagus testacea*	Gall-makers
		Apocryptophagus mayri	
		Apocryptophagus agraensis	
	Pteromalidae	*Apocrypta westwoodi*	Parasites and inquilines
		Apocrypta sp.	
Ficus benjamina	Agaonidae	*Eupristina koningsbergeri*	Pollinators
	Pteromalidae	*Walkerella benjamini*	Gall-makers
		Walkerella sp.	
	Epichrysomallinae	*Sycobia* sp.1	Gall-makers
		Sycobia sp.2	
		Sycobia sp.3	
		Acophila sp.	
	Pteromalidae	*Sycoscapter* sp.	Parasites and inquilines
		Philotrypesis tridentata	
		Philotrypesis distillatoria	
		Philotrypesis sp.1	
		Philotrypesis sp.2	
	Eurytomidae	*Sycophila* sp.1	Parasites and inquilines
		Sycophila sp.2	
	Ormyridae	*Ormyrus* sp.	Parasites and inquilines
Ficus auriculata	Agaonidae	*Ceratosolen emarginatus*	Pollinators
	Sycophaginae	*Apocryptophagus* sp.1*	Gall-makers
		Apocryptophagus sp.2	
		Apocryptophagus sp.3	
	Pteromalidae	*Sycoscapter roxburghi*	Parasites and inquilines
		*Philotrypesis longicaudata**	
		Philotrypesis sp.*	
Ficus hispida	Agaonidae	*Ceratosolen solmsi marchali*	Pollinators
	Pteromalidae	*Philotrypesis pilosa*	Parasites and inquilines
		Philotrypesis sp.	
		Apocrypta bakeri	

Note: *Represents that these species of non-pollinating fig wasp reproduce in both female and male syconia.

Methods

Collection of insects: For each fig species, two trees were selected for observation and collection of insects at each sampling site (dieocious species included two female trees and two male trees). Typically, 30 immature figs were marked, and all insects encountered on them were collected during the different developmental periods. We observed and collected insects for two days in the wasp receptive and emerging phases and on a randomly selected five days for insect collection in the immature, developing, and fruiting phases. Collecting times were in the morning (6:00–9:00), at noontime (12:00–14:00) and at dusk (18:00–20:00) on each collecting day. A total of five crops of *F. racemosa* per site, two crops of *F. benjamina* per site, two crops of *F. auriculata* per site, and three crops of *F. hispida* per site were sampled. To collect fig wasps, fine-mesh nylon bags (20 × 20cm) were used to enclose ten figs per tree during the wasp emerging phase. All fig wasps were preserved in 70% ethanol and later identified.

Data analysis

Species diversity was evaluated using Shannon-Weiner's index of diversity (H') and Pielou's evenness index (J').

3. Results

The composition of insect functional groups on four Ficus *species*

We collected 116,719 insects comprising six orders, 23 families, 40 genera, and 65 species. Every fig species was pollinated by unique wasp species. Although pollinators only comprised four species, they comprised 66% of the total number of individuals collected. Each fig species also harbored several non-pollinating wasps. In total, the four species of figs harboured 28 species of non-pollinating fig wasps, with the monoecious contributing most (Table 1).

Table 2. The communities of other insects collected from four species of figs at Xishuangbanna, China.

Orders	Families	Insect species	Functional groups of insects	*Ficus* species
Hymenoptera	Formicidae	*Polyrhachis vicina*	2	abcd
		Oecophylla smaragdina	2	abcd
		Tetraponera microcarpa	12	a
		T. rufonigra	12	abc
	Vespidae	*Vespa auraria*	12	abcd
	Polistidae	*Polistes olivaceus*	12	abcd
		P. adustus	12	abcd
Coleoptera	Staphylinidae	*Paederus idea*	2	cd
		P. fuscipes	2	cd
	Coccinellidae	*Scymnus longisiphonulus*	2	abcd
	Curculionidae	*Curculio chenensis*	1	abcd
Lepidoptera	Carposinidae	*Heterogyman* sp.	1	cd
	Nymphalidae	*Kallima inachus*	1	abcd
	Cossidae	*Xyleutes mineus*	1	abcd
	Noctuidae	*Oraesia emiarginata*	1	abcd
		Calesia dasyptera	1	abcd
		Anomis fulvida	3	abcd
		Adris tyrannus	3	abcd
		Hypena abyssinalis	3	abcd
	Nymphalidae	*Kallima inachus*	3	abcd
		Cynthis cardui	3	abcd
		Ariadne ariadne	3	abcd
Homoptera	Diaspididae	*Pseudaonidia duplex*	3	abcd
		Hemiberlesia cyanophylli	3	abcd
		Aspidiotus destructor	3	abcd
	Fulgoridae	*Geisha distinctissima*	3	acd
	Aphididae	*Cinara grossa*	3	abcd
Diptera	Cecidomyiidae	*Horidiplosis* sp.	Gall-makers	b
	Trypetidae	*Dacus* sp.	1	abcd
		Bactrocea occipitalis	1	abcd
	Drosophilidae	*Drosophila nasuta*	4	abcd
		D. immacularis	4	abcd
Hemiptera	Pyrrhocoridae	*Dindymus rubiginosus*	3	cd

Notes: 1: Pulp eater; 2: Predator; 3: Sap feeder; 4: Decomposer. a: *Ficus racemosa*; b: *F. benjamina*; c: *F. auriculata*; d: *F. hispida*.

Table 3. Insect species richness, Shannon diversity index (H'), and Pielou's evenness index (J') for different fig species at Xishuangbanna, China.

Ficus species	Number of species (S)	Index of diversity (H')	Index of evenness (J')
F. racemosa	36	0.608	0.170
F. benjamina	24	0.110	0.035
F. auriculata	46	1.181	0.308
F. hispida	36	0.281	0.078

Table 4. Insect species richness, Shannon diversity index (H'), and Pielou's evenness index (J') in different forest types for insects collected from four fig species at Xishuangbanna, China.

Sampling site	Number of species (S)	Index of diversity (H')	Evenness of species (J')
Primary rainforest	51	0.781	0.199
Ravine rainforest	50	0.745	0.194
Secondary forest	41	0.718	0.191

According to their behaviour and feeding pattern, others insects were divided into four functional groups. Thirteen species, representing only 0.57% of individuals collected, were pulp eating insects, including moths, ants etc. As expected, in dioecious figs, pulp eating insects mainly fed on female figs. Only twelve species, 1.21% of insects collected, were sap feeders. They were mainly moths, butterflies, coccids, aphids and bugs. They often induced fig abortion and also ate mature figs which accelerated fig rot. Ten species, 6.72% of the insects collected, were predators. They not only preyed on fig pests, but also ate fig wasps. These insects included four species of ants, three species of preying wasps, and three species of beetles. Only two species, 7.68% of insects collected, were decomposers. They were fruit flies (*Drosophila*) and ate mature or rotten figs (Fig. 1, Table 2).

Diversity and evenness of insect communities found on different fig species

Inflorescence size and position determined the diversity and structure of the insect communities found on each fig species (Table 3). *Ficus auriculata* had large cauliflorous figs and many pulp eating insects were found on the fruits. The richness, diversity and Pielou's evenness index of insects was highest on *F. auriculata*, of the four fig species examined. In contrast, figs of *F. benjamina* are borne in the leaf axils and were the smallest, and the richness, diversity and evenness index of the insect community was the lowest.

Diversity and evenness of insect communities in different forest types

The diversity of species was, as expected, highest in the primary rainforest, and lowest in secondary forest (Table 4). The evenness of the community followed a similar pattern. In going from primary to secondary forest there was a loss of ten species.

4. Discussion

Previous research on the insect communities associated with fig inflorescences has only focused on pollinating and non-pollinating fig wasps (West et al., 1994; Kerdelhué et al., 2000). Shanahan et al. (2001) reviewed fig-eating by vertebrate frugivores for the 260 *Ficus* species, but studies of other functional groups feeding on fig inflorescences are few. Novotny's team published detailed work on the herbivorous insects on figs in Papua New Guinea. They divided species into leaf-chewing and sap-sucking insects, and found a high faunal overlap among communities on different *Ficus* species (Basset and Novotny, 1999;

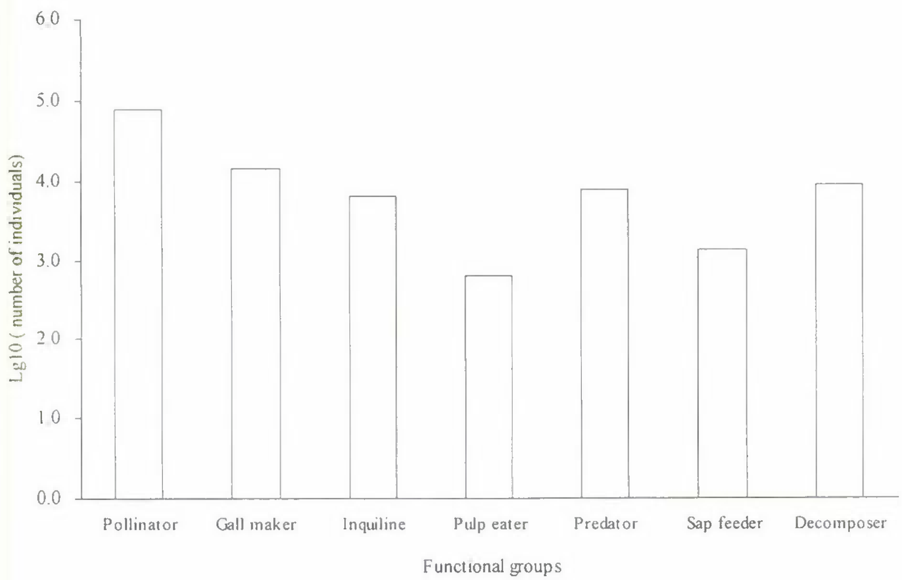

Figure 1. The individual distribution in different insect functional groups at Xishuangbanna, China.

Novotny et al., 2000). The replication of a similar resource across different species of a pan-tropical genus that is ubiquitous in lowland tropical rain forests (Harrison, 2005), makes the study of these communities interesting.

Furthermore, the factors that determine the structure and diversity of insect assemblages can be investigated. Our results show that figs and their associated insects groups comprised a complex micro-ecological system. Different insect groups utilize the figs at different developmental phases. We have collected the complete fig wasp assemblages found a very high degree of specificity. In contrast, across fig species pulp eaters, predators, sap feeders, and decomposers exhibited a similar community structure and there was a high degree of overlap between different fig species.

However, beetles, coccids and bugs varied substantially in abundance and diversity between fig species. For example, *Horidiplosis* sp. (Cecidomyiidae) made galls inside the inflorescence, and only attacked *F. benjamina*. The size of the fig inflorescence and its position largely determined the structure of these functional groups. Many species of insect obtain their sustenance and living space from figs, and thus figs play an important role in promoting insect diversity, as well as that of fruit-eating vertebrates (Shanahan et al., 2001).

Previous studies have reported that a few non-pollinating wasps enter the fig to oviposit (Kerdelhué et al., 2000; Jousselin et al., 2001). We found that all the non-pollinators in Xishuangbanna oviposited by inserting their ovipositors through the fig wall from the outside. However, contrary to most previous reports, we found that three non-pollinating species oviposited on the female figs of *F. auriculata* and produced viable offspring (Weiblen et al., 2001; Peng et al., 2005). Non-pollinating fig wasps comprised a small, but specialised community. Little is known about their basic natural history and these wasps would be worth investigating further.

The fig-associated insects were most diverse and abundant in areas where the tropical rainforest was best preserved. Although the fig species studied here were found in both primary and secondary forests, many of the inflorescence-associated insects may depend on resources restricted or largely restricted to good quality forest. More specialized insect species may be affected by fragmentation of the forests that result in increasing distances, between flowering fig trees and more barriers to dispersal. Fig inflorescences are a comparable resource that is present in most moist tropical habitats, across environments that have been subjected to different levels of human disturbance. Figs, thus, present us with an ideal material and opportunity to understand how insect assemblages are structured in both natural and disturbed environments.

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