

Seasonal change in the structure of fig-wasp community and its implication for conservation

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Abstract

Figs (Moraceae) and their pollinating wasps (Agaonidae) constitute a famous reciprocal mutualism in which figs provide some female flowers for the development of fig wasp offspring while the fig wasps pollinate fig flowers. However, figs also host many non-pollinating wasps which are either parasitoids or resource competitors of pollinators, and bring no benefit for figs and are detrimental to fig's fitness. Our data on *Ficus racemosa* in Xishuangbanna showed that the numbers of non-pollinators and the mature syconia without pollinator wasps increase in rainy season, especially in the highly fragmented forest. This might be because of the longer developing time of the syconia and thereby longer oviposition time to non-pollinators in the dry season. The galled flower and the viable seed percentages in dry seasons are also larger than in rainy seasons in both primary forest and fragmented forest, and the development of non-pollinators is mainly at the expense of pollinator wasps. Our results showed that there exists a discriminative seasonal impact of non-pollinators and fragmentation effects on population size of fig's pollinators. This implies that fig/fig wasp mutualism is more fragile in dry season, and that the critical population size and breeding units of figs in seasonal area might be larger than previously estimated without considering the seasonal change of pollinator population.

Keywords: Fig, tropical rain forest, seasonal change, community structure, mutualism, conservation

1. Introduction

As keystone tropical plant resources in tropical rain forest, figs fruit all year round and support a broad spectrum of vertebrate frugivores during times of food scarcity in these areas (Janzen, 1979; McKey, 1989; Nason et al., 1998; Shanahan et al., 2001). The figs therefore can greatly influence the system structure and function of the tropical rain forest (Krebs, 1978; Nason et al., 1998; Primack, 1998; Thornton et al., 1996; Harrison, 2005). However, what constitutes effective breeding units and critical population size (CPS) of these species hasn't been directly addressed until now (McKey, 1989; Nason et al., 1998; Bronstein et al., 1990; Anstett et al., 1995). Obviously, the effective breeding unit and CPS of these keystone species depend on the population sizes of both figs and their species-specific pollinators (Kjellberg and Maurice, 1989; Bronstein et al., 1990; Anstett et al., 1995). So, the information on the pollinator wasp population has very important implications for our understanding on what

the effective breeding unit and CPS of these keystone species are.

In the obligate mutualism between figs and their pollinator wasps, the pollinator wasps carry pollen from mature syconia to receptive syconia (enclosed inflorescences), while the figs provide their pollinators some of their female flowers for oviposition. The larvae of pollinating wasps develop to be adults in galled female flowers. Adult female wasps developed in the syconia will then disperse with pollen from their natal fig. Both pollen dispersal (from mature syconia) and pollen availability (to receptive syconia) therefore depend on the highly specific pollinator wasps (Herre and West, 1997; Wiebes, 1979; Wang et al., 2008). The figs' female flowers can also be galled by many non-pollinators (Kerdelhué and Rasplus, 1996; Kerdelhué et al., 2000; West and Herre, 1994; West et al., 1996). The competition for the available female flower resource between fig's pollinators and non-pollinating wasps or the parasitizing of non-pollinators on pollinators will negatively affect the pollinator wasp population, which may influence the effective breeding units and the CPS of figs. Unfortunately, this topic has

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received little attention.

In the reported figs, most of the non-pollinators are the resource competitors of the pollinators (Janzen, 1979; Kerdelhué et al., 2000; West and Herre, 1994). Usually, only one larva per ovary can be found. The non-pollinators are either parasitoids of the pollinator wasps, or resource competitors of which may be gall makers or inquilines competing for the ovipositing flowers or nutrition of ovary with pollinators (Kerdelhué et al., 2000; West and Herre, 1994; Wang and Zheng, 2008). In addition, in many figs, the non-pollinator numbers are negatively correlated with the numbers of pollinators (Janzen, 1979; West and Herre, 1994; West et al., 1996; Wang et al., 2005a). Obviously, the population size of the non-pollinators can directly influence the population size of the pollinators (Compton and Robertson, 1988; West and Herre, 1994; Bronstein, 2001; Wang et al., 2005b). To figs, if there existed shortage of the pollinators, the shortage of pollinators to receptive syconia will not be always identical all over the year in seasonal tropical rain forests (McKey, 1989).

In the tropical rain forest, many fig species differ greatly in fruit abundance between the rainy and dry seasons. In some of the fig species, such as all the hemi-epiphytes, they have only small retarded crops in the dry season or winter (Janzen, 1979; Bronstein, 1989). Most of the figs bear their fruits during the warmer months and just have sufficient production over the winter to allow insect propagation (Janzen, 1979). Because of resource limitation, the pollinators and the non-pollinators experience a bottleneck at the same period, namely, in winter or during the dry season (Wang et al., 2008). The community structure in the bottleneck period is one of the critical points in our understanding of what constitute the effective breeding units and the CPS of these keystone species.

Here, we examine the fig wasp community in different seasons in *Ficus racemosa*. We address three questions: (1) Are the seasonal effects identical on the pollinators and non-pollinators? (2) Are there differences of the impact of non-pollinators on the pollinator offspring and the viable seeds? and (3) Do different habitats have effects on the wasp community structure?

2. Materials and Methods

Sample sites

Our work was carried out in Xishuangbanna, Yunnan, China. This sample site is in the south of Yunnan province (21°41'N, 101°25'E), where the altitude is about 600 m and the climate presents a rainy and dry season. In Xishuangbanna, the rainy season last from May to October. The annual precipitation is 1,557 mm and about 80% of the total yearly rainfall occurs during the rainy season (Yang et al., 2001). Monthly temperatures are low from November to

January, and January is the coldest month with a monthly average temperature of 12.5°C.

We collected the samples from both primary forest and fragmented forests in which the trees of *F. racemosa* mainly distribute near water. The sampled primary forest is about 100,000 ha. The *F. racemosa* trees distribute in primary forests very sparsely, and we have not found other groups within 2 km in our sampled forests. While, the trees of *F. racemosa* can be easily found in the small fragmented forest (fragmented in 60s) and the edge of the primary forest within 1 km, usually no more than 500 m from each other. The trees of *F. racemosa* distribute in a relatively high density in the fragmented forests and the edge of primary forest compared with the interior of primary forest. In Xishuangbanna, the fragmented forests are usually no more than 2 km². They are mainly fragmented by crop field, road and rubber forests.

Study species

The monoecious fig *F. racemosa* (*F. sycomorus*) is distributed from India to Australia (Corner, 1965). *Ficus racemosa* is a large tree that can reach 30 m, and bear cauliflorous syconia in a very large number. It mainly grows in the moist valleys or along rivers. The trees of *F. racemosa* usually are of groups with each group consisting of 5–10 trees in primary forest (Yang et al., 2000). The density of the syconia in the dry season is much lower than during the rainy season in both primary forest and fragmented forest, and some trees that are not of groups might not bear syconia in the highly fragmented area. From the end of April or early of May, most of the trees begin to fruit in a large numbers and the trees that did not bear syconia also begin fruiting in this period. In Xishuangbanna, the syconia of *F. racemosa* need no more than 1 month to complete their fruiting cycle in the rainy season. In the dry season, they may need 2 or 3 months to complete their fruiting cycle.

Ficus racemosa is pollinated by *Ceratosolen fusciceps* (Agaonidae). The foundresses (pollinator being syconium) number per fruit in *F. racemosa* is relatively large, and can be more than 80 in some extreme cases. As to the non-pollinators in *F. racemosa*, there are three species of *Apocryptophagus* (Sycophaginae) and two species of *Apocrypta* (Sycoryctinae). The genus of *Apocryptophagus* including *A. testacea* and *A. mayri* are gall maker, and the genus *Apocrypta* including *A. sp.* and *A. westwoodi* are parasitoids of *Apocryptophagus testacea* and *A. mayri* separately. *Apocryptophagus agraensis* might be parasitoid of pollinator wasps (Kerdelhué and Rasplus, 1996; Kerdelhué et al., 2000; Wang and Zheng, 2008). All kinds of the male wasps in *F. racemosa* are wingless (Kerdelhué et al., 2000). The non-pollinator wasps do not enter the cavities of the receptive fruits to lay eggs and oviposit into the female flowers from outside of the syconium wall.

Methods

At the pre-D stage of the syconium development, it is the best time to count the flowers, because the seeds and galls are easy to distinguish in this period. The syconium diameters can also be collected from the same syconia, for the syconia stop to grow in this period. Data on adult wasps were collected in the same crops with that of the seeds and galls. When the syconia were mature, and they still had no exit holes, we collected them from two sample sites (primary forest and highly fragmented area) and took them back to lab. We inject 75% alcohol into the cavities to kill the adult wasps, and then cut open syconia to count the adult wasps. All of the adult wasps per syconium were collected separately. The male wasps of *Apocryptophagus* are very tiny and difficult to distinguish, so, only female wasps of all of fig wasps are entered in our data analyses.

All of the data were collected from two sample sites, and the same sampled trees were selected at different seasons. One set of data was from the center of primary forest, and the other set of data was from the highly fragmented forest. We selected two sample sites in the primary forest and three sample sites in the fragmented forests. Because the fig trees usually bear syconia synchronously within groups, we usually only collected the sample syconia from 2 trees in primary forest and 3 trees in fragmented forests in each month. In the adult wasp data collection, the number of sampled syconia of primary forest is 68 in rainy season and 39 in dry season; whilst the number of sampled syconia of fragmented forest is 69 in rainy season and 88 in dry season. In the viable seed and gall data collection, the number of sampled syconia of primary forest is 20 in both rainy season and dry season; whilst the number of sampled syconia of fragmented forest is 18 in rainy season and 20 in dry season.

In the same crops with the data of viable seeds and galls, data of foundress number were collected from the receptive fruits. After the fruits enclose their bracts and no more pollinators can enter the fruits, we cut open the fruits to count the remains of foundresses. The data of viable seeds, galls, and foundresses number per fruit are collected in May and July in rainy season, and from November to January in dry season over one year

Statistics

All the census data were analyzed by the SPSS 10.0 software. The correlation between the foundress number and the gall and seeds was analyzed with Pearson correlation. The mean comparison analyses on the percentages of all kinds of wasp in the community were used with t-test. Because the fruit diameter is different among different sample sites and season and thereby the mean number of galls and viable seeds per fruits is also different greatly, we compared the mean number of galls

and viable seeds between the samples and seasons included the fruit diameter as covariate (GLM).

3. Results

The data in Table 1 show that the mean percentages of female pollinating wasps in the dry season are much smaller in both sample sites, while the percentages of *Apocryptophagus* and *Apocrypta* wasps in the dry season are larger than in rainy season, at the expense of pollinator wasps (Table 2). The total number of the wasps per fruit in the dry season is significantly lower than in rainy season in the primary forest ($t = 2.77$, $df = 124$, $P < 0.01$). In the fragmented forests, the total number of the wasps per fruit in the dry season is not significantly lower than that of the rainy season. The mean number of pollinators in the dry season is significantly lower than that in rainy season in both primary forest ($t = 3.29$, $df = 124$, $P < 0.001$) and fragmented forests ($t = 2.25$, $df = 128$, $P < 0.05$).

Observation shows that the fruiting cycle in the dry season is much longer than in rainy season. In the rainy season, only a few syconia have galls (only oviposited by non-pollinators) before pollinators enter the receptive syconia, and the mean number of galls per receptive syconia is 7 ($n = 120$, the oviposition of non-pollinators mainly occurs after the pollinators enter in the receptive syconia). In the dry season, however, it is very common that the receptive syconia have galls before pollinators entering syconia and, the mean number of the galls per receptive syconium was 17 ($n = 105$), implying that the developmental time can ensure the gall development in dry season while not in warm season. Usually, the fruiting cycle of *F. racemosa* is about 1 month in the rainy season, whilst it can last about 2 or 3 months in the dry season much longer than in raining season. The time during which non-pollinators can oviposit is much longer in the dry season than in the rainy season.

The mean numbers of galls per syconium in the dry season was higher than in rainy season in both primary forest and highly fragmented area (Table 3). The comparison using the mean number of galls per syconium between the rainy season and dry season shows that, including the diameter of syconia as covariate, both sites had significant differences between wet and dry seasons but the size of the difference was greater in the fragmented forest seasonality (Table 4). In the highly fragmented area, the mean foundress number per syconium in the rainy season (10.7 ± 6.0 , $n = 34$) is higher than in dry season (7.8 ± 3.3 , $n = 51$) and crop mean foundress numbers significantly differ between season ($df = 83$, $P < 0.005$). But in the primary forest, the mean foundress number in rainy season (34.7 ± 24.7 , $n = 40$) is also larger than in dry season (22.4 ± 18.8 , $n = 47$). The pollinator wasp population in primary forest is significantly higher than in highly

Table 1. The number (mean \pm SD) and percentage (%) of all kinds of adult female wasps in mature fruits (*F. racemosa*) from different sample sites in different seasons.

Seasons	Sampled trees	Sampled fruits	Pollinators (%)	<i>Apocryptophagus</i> wasps (%)	<i>Apocrypta</i> wasps (%)	Non-pollinators (%)
Samples from primary forest						
Rainy	4	68	419 \pm 446.3	83 \pm 77	13 \pm 10	96 \pm 80
			70.3 \pm 22.4	24.1 \pm 18.9	5.4 \pm 6.2	29.6 \pm 22.4
Dry	4	39	163 \pm 199	79 \pm 63	42 \pm 36	121 \pm 85
			47.7 \pm 27.7	34.4 \pm 21.2	17.8 \pm 13.5	52.3 \pm 27.7
Samples from fragmented forests						
Rainy	6	69	335 \pm 369	82 \pm 80	13.5 \pm 13	95 \pm 84
			66.6 \pm 23.3	26.8 \pm 19.0	6.5 \pm 8.8	33.4 \pm 23.3
Dry	7	88	111 \pm 170	82 \pm 80	42 \pm 35	122 \pm 82
			35.4 \pm 28.0	43.7 \pm 24.2	20.8 \pm 14.7	64.6 \pm 28.0

The non-pollinators include both *Apocryptophagus* wasps and *Apocrypta* wasps.

Table 2. Comparisons of the mean percentages of pollinator wasps and non-pollinator wasps in the total fig wasps supported by *F. racemosa* between the rainy season and dry season by Student's t-test in both primary forest and fragmented forest.

Sample	Pollinators	<i>Apocryptophagus</i>	<i>Apocrypta</i>	Non-pollinators
Primary forest	4.6***	2.5**	6.4***	4.6***
Fragmented area	7.5***	4.7***	7.4***	7.4***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

fragmented area, for the foundresses number is positively correlated with wasp offspring number ($n = 65$, $r = 0.48$, $P < 0.001$).

The data also show that the mean numbers of galls and seeds of pre-D phase syconia in the dry season are also significantly higher than in rainy season, and the percentages of galls and viable seeds in the total female flowers in the dry season are also larger than the rainy season in both primary forest and fragmented forest (Table 3). The data indicate that higher non-pollinators in fig-supported wasp community do not lead to fewer viable seeds. The negative effects of non-pollinators on viable seeds are not obvious in *F. racemosa* in natural condition.

We also collected the proportions (R) of the mature fruits without pollinator wasps in their fruit cavities in all of the developed fruits. In the rainy season, the difference of the proportions between the trees from primary forest ($n = 210$, $R = 2.34\%$) and the trees from fragmented area ($n = 320$, $R = 4.12\%$) is not so large. In the dry season, however, the difference of percentages between the trees from primary forest ($n = 184$, $R = 3.33\%$) and trees from highly fragmented forests ($n = 265$, $R = 19.65\%$) is very large. In some extreme cases, the trees of fragmented forests can bear 33.25% ($n = 120$) fruits that only oviposited by non-pollinators. The shortage of pollinators in the dry season is more severe in the highly fragmented areas.

4. Discussion

In the fig/fig wasp mutualism, fig and its pollinator interaction might be more fragile than other species interaction because of a fig obligate mutualism (Bronstein and Maurice, 1989; Wiebes, 1979). The establishment and maintenance of fig population must depend on a critical minimum number of their obligate pollinator wasps (McKey, 1989; Nason et al., 1998). The pollinators probably have difficulty in seasonal sites because (1) fig trees flower rarely in winter; (2) trees that do flower are less detectable and more difficult to reach in winter or dry season (Bronstein, 1989).

Our data show that non-pollinators further exacerbate the problems of maintaining pollinator populations in the seasonal sites. Usually, the non-pollinators oviposit from the outside of syconia and can oviposit during a much longer time than pollinator wasps, while the pollinators must oviposit in the fruit cavities and only live 1 or 2 days after exiting galls (Bronstein, 1989, 1991; Kerdelhué and Rasplus, 1996; Nason et al., 1998). In the dry season (winter), the development time of fig syconia is much longer than in rainy season (warmer in climate), which result in longer time for non-pollinators to oviposit.

However, the ovipositing time length to pollinators is not changed a lot. The non-pollinators will lead to less production of pollinating wasps, because the non-pollinator wasps tend to oviposit flowers already oviposited by pollinators or directly parasitize the offspring of pollinators (Bronstein, 1991; Kerdelhué and Rasplus, 1996; West and Herre, 1994; West et al., 1996; Wang and Zheng, 2008). Hence, the increased non-pollinator wasps in the dry season will exacerbate the pollinator supply, which might make interaction between the figs and their pollinators more fragile, especially in the fragmented forest. The mechanisms that might disrupt or maintain the fig/fig wasp system might work in this bottleneck period (Colinvaux, 1986; Sun, 1992).

Table 3. The number of galls and seeds per fruit (mean \pm SD) and the percentages of them in the total female flowers per fruit (*F. racemosa*) from different sample sites in the rainy season and dry season.

Sample sites	Sample size	Diameter	Galls per fruit	Seeds per fruit	PG (%)	PS (%)
Data from rainy season						
Primary forest	20	3.78	1780.9 \pm 918.9	1539.9 \pm 765.0	28.2 \pm 10.4	24.8 \pm 11.2
Fragmented area	18	3.85	1906.8 \pm 220.9	2303.8 \pm 383.3	30.7 \pm 11.9	27.9 \pm 10.9
Data from dry season						
Primary forest	20	3.98	2054 \pm 409.4	2410.4 \pm 717.4	32.9 \pm 2.7	37.3 \pm 2.6
Fragmented area	20	3.92	2599.2 \pm 699.4	2483.1 \pm 460.6	41.1 \pm 7.3	40.4 \pm 9.1

PG is the percentage of galls in the total female flowers per fruit and the PS is the percentage of seeds in the total female flowers per fruit. The total number of female flowers per fruit ranged from 4088 to 12413 (N = 108). The sample fruits are from 4 trees in each season.

Table 4. Comparison of the mean numbers of galls and seeds from the premature fruits (*F. racemosa*) between different seasons and different sample sites (GLM) included diameters as covariates.

Comparison between rainy season and dry season				
Sample site	Crops	N	Galls	Seeds
Primary forest	2	41	28.28***	14.45***
Fragmented area	2	38	61.35***	1.85 ns

Comparison between different sample sites				
Seasons	Crops	N	Galls	Seeds
Rainy season	2	39	23.05***	12.02***
Dry season	2	40	37.28***	3.30*

* $P < 0.05$, *** $P < 0.001$, ns = not significantly different at $P = 0.05$.

Our study also show that the forest fragmentation greatly affect the community structure of the fig wasps in figs and thereby might affect the interaction between figs and fig wasps, especially in the dry season. In the fragmented area, pollinator abundance in the fragmented area is lower than in primary forest (Wang et al., 2005a), which might result in two negative effects on the figs' and the pollinators' population maintenance. First, less pollen dispersion from mother trees and shortage of pollinator supply to receptive trees, and thereby less viable seed production and more un-pollinated syconia. Second, because fewer foundresses enter each syconium, higher inbreeding will be, pollinators are forced to mate with siblings before they exit the mature fig fruits (Janzen, 1979; McKey, 1989). Both of these might result in the local disruption of the pollinator population, provided such fragmentation and inbreeding effects can be accumulated in the process of evolution. These two effects are more obvious in the dry season. Giving enough attention on such effects on these keystone species is very necessary in determination on how large an area can keep the tropical rain forest stable (Stockwell et al., 2003).

Bronstein and her colleagues (1990) developed a model on the CPS of *Ficus* with the data on the flowering traits in equatorial tropic forest, and their model showed that 95 trees are required to produce an asynchronous sequence that could maintain local pollinator population for 4 years. They suggested that, in the seasonal site, both the critical population size (CPS) and the probabilities of reproductive failure to figs and pollinator wasps will be larger than those of the equatorial site for the gap occurring in the flowering sequence (Bronstein et al., 1990). Nason and his collaborators' work showed that the pollen dispersion distance can reach 5.8–14.2 km and the breeding units of figs comprise hundreds of intermating individuals distributed over areas of 106–632 km² as a result of extensive pollen movement (Nason et al., 1998). In fact, the breeding structure of figs and the interaction between the figs and their pollinator wasps are more fragile with the increase of the amplitude of the seasonality and it may be more difficult to protect them from local extinction in the highly seasonal sites in applied conservation effort (Bronstein et al., 1990; Anstett et al., 1995; Wang et al., 2005a).

Our study show that the negative effect of non-pollinators and fragmentation effect on the pollinators might be more severe in the dry season, which further might exacerbates the maintenance of pollinator's population. Given the consideration on effect of non-pollinators on the pollinators in the bottleneck in the dry season and the fragmentation effects on both figs and their pollinator wasps, the CPS of both figs and their pollinating wasps and figs' breeding units might be larger than previously estimated. The probabilities of reproductive failure will increase greatly in seasonal area, and the situation will be more severe in the fragmented forest.

Many previous works showed that the seasonality and other environmental change result in the shortage in the pollinator supply to the receptive trees (Bronstein, 1991; Compton, 1994; Anstett et al., 1996; Bronstein and McKey, 1996). Our study might suggest that the fragmentation and the negative effect of the non-pollinators might also result in the shortage in the pollinator supply to the receptive trees in the dry season. In the primary forest, the percentage of

mature fruits without pollinator wasps in their cavities is very low all over the year, but it is high in the fragmented forest in the dry season. The data in this study and other work (e.g. Wang et al., unpublished data) may suggest that there is very little shortage of pollinators in the rainy season but there exists in the dry season. In the dry season, the percentage of mature fruits without pollinators is higher than in rainy season and the percentage in the rainy season is very low. These data indicate that the shortage of pollinator supply to the figs' receptive syconia exists in the dry season, but it mainly exists in the fragmented area.

The higher mature fruits without pollinator wasps in the fragmented forest imply that the fragmentation effect might stop the reciprocal interaction between the figs and their pollinator wasps. The data in this study also imply that the fig/fig wasp system possibly transforms to be parasite-host system between figs and non-pollinators in the fragmented area, which is a dangerous hint to our conservation effort to this key stone plant resource. This set of data also involves in another heated question on what may keep plant fruits from abortion, no matter in figs or in other plants (Stephenson, 1981). Herre assumed the fig fruits might abort without pollination in some specific situation (Herre, 1989). The data on *F. racemosa* show that there are many syconia that only oviposited by non-pollinators still develop to be mature fruits and do not abort, especially in the fragmented forest (Wang et al., 2005b; Wang and Zheng, 2008; Sun et al., 2008). The experiment of us shows that the fig only abort the fruits oviposited by some specific non-pollinators (Sun et al., 2008), and that the syconia oviposited by pollinators without pollination do not abort in both *F. racemosa* and other figs (Joussellin et al., 2003; Wang and Zheng, 2008; Sun et al., 2008). Because the non-pollinators have no fitness to fig (West and Herre, 1994; West et al., 1996), the factors that keep figs support the un-pollinated syconia developed to be mature fruits may be important in disclosing how the fig/fig wasp system maintains stable.

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