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A species of fig tree and three unrelated fig wasp pollinators

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ABSTRACT

Background and question: A few non-agaonid wasps can enter figs to oviposit and effectively pollinate their fig hosts. In Xishuangbanna (Yunnan, SW China), *Ficus curtipes* is passively pollinated by an undescribed *Eupristina* species (Agaonidae). Two species of non-agaonid fig wasps, *Diaziella yangi* and *Lipothymus* sp., also enter the fig to oviposit. Yet such wasps do not establish a mutualistic relationship with figs similar to that of agaonids. Why?

Method: Using controlled experiments in which only one foundress per species was introduced to a fig, we compared the effect of the three wasp species on pollination. We recorded foundress distribution in the fig female floral phase, and counted the number of wasps and seeds in the male floral phase.

Results: *Diaziella yangi* and *Lipothymus* sp. follow *Eupristina* sp. into the figs, and both non-agaonids are efficient pollinators. In nature, most figs were entered by just one species of foundress: 36% were entered by *Eupristina* sp. only, 8% by *D. yangi* only, and 3% by *Lipothymus* sp. only. About 28% of adult fig wasps emerging from figs were *D. yangi*, 4% were *Lipothymus* sp., and 65% were *Eupristina* sp.; ten other non-agaonids ovipositing from outside the fig comprised just 3% of the adult wasps that emerged from figs. Both species of fig-entering non-agaonid wasps significantly reduced the number of *Eupristina* sp. emerging from mature figs but had no effect on seed production. If *D. yangi* or *Lipothymus* sp. was introduced to figs containing one foundress of *Eupristina* sp., both non-agaonid wasps produced offspring. But without the *Eupristina, D. yangi* and *Lipothymus* sp. failed to reproduce. *Diaziella yangi* and *Lipothymus* sp. depend on the agaonid, *Eupristina*, to make galls.

Conclusion: Because they depend on the legitimate pollinator to make galls, neither *D. yangi* nor *Lipothymus* sp. is able to replace the agaonid wasp and establish a mutualistic relationship with their host fig.

Keywords: *Ficus*, mutualism, non-pollinating fig wasps, parasitism, pollinating fig wasp.

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INTRODUCTION

The interaction between fig wasps (Agaonidae) and their host fig trees (*Ficus*) is a striking example of an obligate plant–insect mutualism (Janzen, 1979; Weiblen, 2002). Seed production by fig trees is dependent on their highly specific pollinating fig wasps, whose offspring feed on a proportion of the fig ovules (Ramirez, 1970; Wiebes, 1979; Rasplus, 1996; Weiblen, 2002; Molbo *et al.*, 2003). The relationship between *Ficus* and their pollinating fig wasps is widely regarded as a model system for studying co-evolution and co-speciation between insects and plants (Jousselin *et al.*, 2003; Weiblen, 2004).

Approximately half of the 750 known *Ficus* species in the world are monoecious, while the rest are functionally dioecious (Berg, 1989; Weiblen, 2000). In monoecious species, both seeds and pollinators develop within the same syconium (fig inflorescence, hereafter referred to as fig). In addition to the mutualistic wasps, fig trees have a suite of non-pollinating wasps whose basic biology is largely undescribed. These so-called non-pollinating fig wasps belong to other chalcidoid families. Most non-pollinating fig wasp species oviposit from outside through the wall of the fig, some are gallers, others are inquilines and parasitoids (West and Herre, 1994).

Only a few non-pollinating fig wasp species can enter figs to oviposit. These internal ovipositing wasps have morphological adaptations similar to those of agaonid wasps for entering figs, such as flattened heads, smooth bodies, and spurs on the legs (van Noort and Compton, 1996). The wasps of *Diaziella* (Sycoecinae) and *Lipothymus* (Otitesellinae) were reported to enter figs and oviposit in the female flowers, just as the pollinator does. They are associated with passively pollinated *Ficus* from section *Conoscycea* and may act as efficient pollinators (Jousselin *et al.*, 2001). Passively pollinated *Ficus* species have high anther-to-ovule ratios (> 0.19), and the pollinators lack coxal combs on the fore coxa and do not load or deposit pollen actively, whereas active pollinators perform pollination with coxal combs on *Ficus* species with low anther-to-ovule ratios (< 0.16) (Kjellberg *et al.*, 2001, 2005). Moreover, the high degree of morphological convergence suggests that *Diaziella, Lipothymus*, and pollinator (Agaoninae) have co-evolved with their host *Ficus* species (van Noort and Compton, 1996). Previous studies have reported that internally ovipositing non-pollinating wasps enter figs at the same time as pollinating wasps. Hence these wasps' natural history is very similar to that of the pollinator (Galil and Eisikowitch, 1969, 1970; Jousselin *et al.*, 2001). Fig-entering non-agaonid wasps seem to be evolutionarily much more recent than agaonids and no situation has yet been found in which they have replaced the agaonid wasps as pollinators (Kjellberg *et al.*, 2005). Why they have been unable to establish a mutualistic relationship with their host figs similar to that of the associated agaonid wasps is unknown. Co-occurrence of pollinating agaonids, *Diaziella* (Sycoecinae), and *Lipothymus* (Otitesellinae) on the same host within the same habitat seems to be common (Jousselin *et al.*, 2001). They show that six species of *Ficus* that are passively pollinated by the agaonid genus *Waterstoniella* host specific wasps belonging to the chalcidoid genera *Diaziella* (Sycoecinae) and *Lipothymus* (Otiteselinae). However, biological data of the internally ovipositing non-agaonids are scarce and their impact on the fig–fig pollinator mutualism is poorly understood.

Ficus curtipes Corner is pollinated by an undescribed *Eupristina* sp. in the Xishuangbanna tropical area. *Diaziella yangi* and *Lipothymus* sp. were also observed to enter the figs and oviposit in the female flowers. In this study, we focused on the following questions: Can *Diaziella yangi* and *Lipothymus* sp. effectively pollinate the figs? Can *Diaziella yangi*

and *Lipothymus* sp. replace the normal pollinator (*Eupristina* sp.)? How does *Diaziella yangi* and *Lipothymus* sp. affect the fig–fig pollinator mutualism?

METHODS

Study site

The study was carried out in the Xishuangbanna Tropical Botanical Garden (101°15′E, 21°55′N), located in south-west China and the northern margin of tropical South-East Asia. The five trees used in the study were distributed in secondary forests.

Study organism

Ficus curtipes belongs to section *Conosycea*. This species is widely distributed in continental Asia (China, India, Malaysia, and Thailand) (Berg and Corner, 2005). Trees grow to 5–10 m in height, but they are epiphytic when young. At Xishuangbanna, this species occurs naturally in tropical forest, but it is commonly cultivated in cities and villages as an ornamental tree. *Ficus curtipes* produces figs in synchronous crops with asynchrony between trees throughout the year. The pollinating wasp (*Eupristina* sp.), two internally ovipositing non-agaonid species (*Diaziella yangi* and *Lipothymus* sp.), and seven externally ovipositing non-pollinating species (including *Sycobia* sp., *Sycoscapter* sp., and *Philotrypesis* sp.) are associated with figs of *F. curtipes*. The anther-to-ovule ratio of *F. curtipes* was 0.84 ($n = 67$), a ratio that indicates passive pollination by *Eupristina* sp. (Kjellberg *et al.*, 2001).

Experimental introductions of the three species of internally ovipositing fig wasps

To ensure that *Eupristina* sp., *D. yangi*, and *Lipothymus* sp. successfully entered a fig, their behaviour was observed in three fig crops (every crop from a single fruiting event of a given tree). In all cases, the three wasps entered the figs on the same day and *Eupristina* sp. entered the fig always earlier than *D. yangi* or *Lipothymus* sp. The time interval between these activities ranged from less than 1 min to 4 h. Attempts to induce *D. yangi* and *Lipothymus* sp. to enter the fig without *Eupristina* sp. were unsuccessful. Based on these observations, we designed the following two kinds of experiments.

From 1 February to 8 May 2007, a suitable tree was located and pre-receptive figs were selected for experimental introduction of *Eupristina* sp. The twigs bearing figs were encased in a fine-mesh nylon bag (200 × 200 mm). Each bag was sealed tightly around the twig to prevent any fig wasps arriving naturally at the tree from pollinating the fig. When the figs reached the receptive phase (12.19 ± 0.57 mm in diameter, $n = 67$), experimental introductions were carried out.

Mature figs were collected on other trees in the vicinity, stored in nylon bags, and the fig wasps allowed to emerge. Foundresses of *Eupristina* sp., *D. yangi*, and *Lipothymus* sp. were collected separately in different bags. The nylon bags were first removed from the experimental twigs. Two kinds of experimental introductions were done: (1) One foundress of *Eupristina* sp. ($n = 17$), *D. yangi* ($n = 18$) or *Lipothymus* sp. ($n = 15$) was introduced directly into a fig. When introducing *D. yangi* and *Lipothymus* sp., *Eupristina* sp. was introduced first. Immediately when its head had entered the ostiole, the wasp was removed and *D. yangi* or *Lipothymus* sp. was allowed to enter the fig. (2) One foundress of

Eupristina sp. was first introduced, then immediately after her introduction, one foundress of *D. yangi* ($n = 11$) or *Lipothymus* sp. ($n = 12$) was introduced directly into same fig. When experimental introductions were finished, the bag was enclosed again on the branch with experimental figs and left until the figs were near maturity. Mature figs were collected and the fig wasps allowed to freely emerge in the bag. The fig wasps were carefully collected and kept in 75% ethanol. The numbers of seeds, and wasps of each species, were counted.

Natural foundress distribution of three species of internally ovipositing fig wasps in female floral phase

One hundred and eighty-four post-receptive figs were collected from three trees (about 60 figs from each tree). In the laboratory, the figs were cut open and the foundress numbers of *Eupristina* sp., *D. yangi*, and *Lipothymus* sp. were determined for each fig.

Natural wasp collection in male floral phase

Ninety-one figs from two trees were collected just before wasp emergence. Each fig was placed individually in a fine-mesh bag (200 × 200 mm) and the fig wasps allowed to emerge. All fig wasps, including the wingless males, were carefully collected and preserved in 70% ethanol. Each wasp was identified to species and counted. The numbers of seeds, aborted galls, and undeveloped flowers were also counted.

Statistical analyses

A paired-samples *t*-test was used to compare offspring of the three species of internally ovipositing fig wasps. Multiple regression models were used to analyse the effects of multiple factors on seed and pollinator production. As the assumptions of normality and equal variance were not met, all data of dependent variables were square root transformed (target variable + 0.5). All analyses were performed in the SPSS (13.0) program.

RESULTS

Non-agaonid wasps can effectively pollinate the figs

Eupristina sp., *D. yangi*, and *Lipothymus* sp. entered figs through the ostiole on the same days during the receptive phase, but *D. yangi* and *Lipothymus* sp. entered the fig always later than *Eupristina* sp. When the individual foundresses of *Eupristina* sp., *D. yangi* or *Lipothymus* sp. were introduced to a fig, one *Eupristina* foundress produced on average 71.41 ± 58.29 (mean ± S.D., $n = 17$) seeds, and both non-agaonid wasps also effectively pollinated *F. curtipes*. Figs pollinated by *D. yangi* produced 40.67 ± 52.31 ($n = 18$) seeds, and figs pollinated by *Lipothymus* sp. produced 70.33 ± 50.67 ($n = 15$) seeds (Fig. 1). The differences in the seeds produced by *Eupristina* sp., *D. yangi*, and *Lipothymus* sp. were not significant ($F_{2,47} = 1.747$, $P = 0.185$).

Successful reproduction of *D. yangi* and *Lipothymus* sp.

When foundresses of *D. yangi* or *Lipothymus* sp. were singly introduced to a fig, no wasp offspring were produced. However, when *D. yangi* and *Lipothymus* sp. were introduced to a

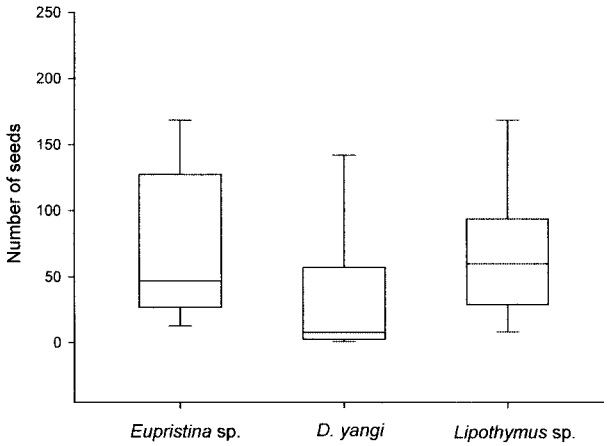

Fig. 1. Number of seeds produced by single foundresses of three species of internally ovipositing fig wasps (17 figs for *Eupristina* sp., 18 figs for *D. yangi*, and 15 figs for *Lipothymus* sp.). Boxes indicate the limits of the 25th and 75th percentiles and the median, the whiskers indicate the total data amplitude.

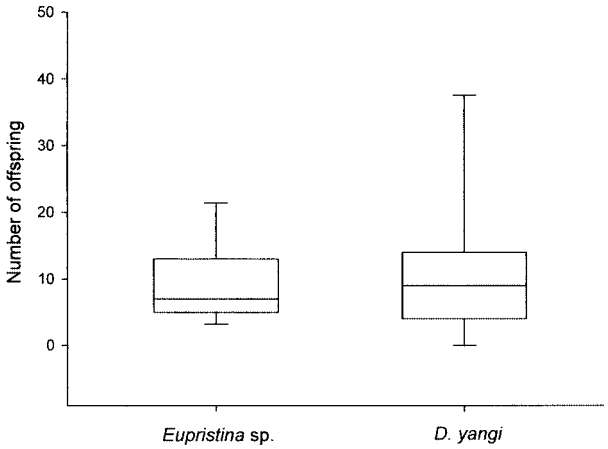

Fig. 2. Offspring production for *Eupristina* sp. and *D. yangi* (11 figs) in figs with a single foundress of each species. Box plot symbols as in Fig. 1.

fig already entered by *Eupristina* sp., both reproduced successfully. In figs entered by *Eupristina* sp. and *D. yangi*, the difference between the numbers of offspring produced by *Eupristina* sp. and *D. yangi* was not significant (*Eupristina* sp.: 9.09 ± 5.96; *D. yangi*: 10.91 ± 11.83; $n = 11$; $t = -0.675$, $P = 0.515$) (Fig. 2). Similarly, in figs entered by *Eupristina* sp. and *Lipothymus* sp., the difference was not significant (*Eupristina* sp.: 6.42 ± 7.25; *Lipothymus* sp.: 11.25 ± 9.28; $n = 12$; $t = -1.548$, $P = 0.15$) (Fig. 3).

How do *D. yangi* and *Lipothymus* sp. affect the fig–pollinator mutualism?

In the naturally entered figs, over 87% of figs contained only one foundress of a species. Two or three co-specific foundresses were rarely found in a fig, and no figs were colonized by

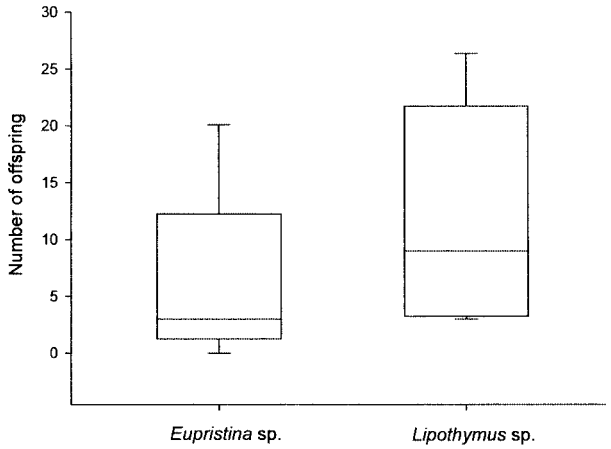

Fig. 3. Offspring production for *Eupristina* sp. and *Lipothymus* sp. (12 figs) in figs with a single foundress of each species. Box plot symbols as in Fig. 1.

more than two foundresses of *Eupristina* sp. Thirty-six percent of figs were only colonized by *Eupristina* sp., 29% by *Eupristina* sp. and *D. yangi*, and 14% by all three species. Figs containing only *D. yangi* or *Lipothymus* sp. were very rare. The emergence of the most common fig wasps in the sampled crops followed the pattern observed for foundress compositions. Among the 91 figs sampled, 57% had only *Eupristina* sp., 34% had both *Eupristina* sp. and *D. yangi*, and 5% had both *Eupristina* sp. and *Lipothymus* sp. Figs with just *D. yangi* comprised just 1% and figs with just *Lipothymus* sp. were not found (Table 1).

With respect to the total fig wasp fauna, ten species, belonging to ten genera of fig wasps, were found among the 9557 wasps collected from 91 figs of *F. curtipes*. The abundance of *Eupristina* sp. per fig was significantly negatively affected by both internally ovipositing non-agaonid species (*D. yangi*: standardized slope = −0.72, $P < 0.001$; *Lipothymus* sp.: standardized slope = −0.38, $P < 0.001$). In contrast, seed production was not significantly affected (*D. yangi*: standardized slope = 0.12, $P = 0.27$; *Lipothymus* sp.: standardized slope = 0.009, $P = 0.39$) (Table 2).

DISCUSSION

Non-agaonid fig wasps that enter figs to oviposit are usually associated with passively pollinated *Ficus* species, and can be efficient pollinators (Jousselin *et al.*, 2001). In all previously studied cases, the natural history of internally ovipositing non-agaonid wasps was thought to be very similar to that of the agaonid wasps (Galil and Eisikowitch, 1969, 1970). Hence, why they do not establish a mutualistic relationship with their host fig similar to that of the associated agaonid wasp is unclear (Herre, 1999). In our study, even though *D. yangi* and *Lipothymus* sp. effectively pollinated *F. curtipes* under controlled experimental conditions, the two non-agaonid wasps could not reproduce independently, and depended on *Eupristina* sp. Although *Eupristina* sp., *D. yangi*, and *Lipothymus* sp. enter the figs on the same day (female floral phase), *Eupristina* sp. almost always enters first. These observations suggest that *D. yangi* and *Lipothymus* sp. are not gallmakers, but inquilines that depend on *Eupristina* to make the galls. This is the first study to suggest why these non-agaonids cannot establish a mutualistic relationship with their host fig similar to that of the associated agaonid wasp.

Table 1. Contents of naturally collected figs (mean ± S.D.)

Species groups	Proportion of natural figs with foundresses	Mature figs sampled	Seeds	*Eupristina* sp.	Non-agaonid wasps	Aborted galls	Undeveloped flowers
Eupristina sp. only	0.36	52	6.92 ± 12.93	104.23 ± 28.79	3.63 ± 14.32	20.90 ± 18.03	143.46 ± 44.12
D. yangi only	0.08	1	16	0	55	8	116
Lipothymus sp. only	0.03	0	0	0	0	0	0
Eupristina sp. + *D. yangi*	0.29	31	9.13 ± 12.18	21.42 ± 27.08	80.19 ± 29.06	20.48 ± 13.46	126.29 ± 49.29
Eupristina sp. + *Lipothymus* sp.	0.08	5	8.40 ± 4.34	18.80 ± 7.89	62.80 ± 15.45	20.00 ± 13.57	181.80 ± 33.31
Eupristina sp. + *D. yangi* + *Lipothymus* sp.	0.14	1	1	5	77	40	87
D. yangi + *Lipothymus* sp.	0.02	1	14	0	83	105	52

Note: Proportion of each species group among foundresses in 184 naturally entered figs. Number of mature figs and their contents, in each species group, among 91 figs collected from two trees.

Table 2. Impact of internally ovipositing non-agaonid species on the production of pollinators and seeds

	Seeds		*Eupristina* sp.	
Variables	Standardized slope	*P* value	Standardized slope	*P* value
D. yangi	0.117	0.267	−0.717	<0.001
Lipothymus sp.	0.092	0.385	−0.373	<0.001

Note: Multiple regression models were used to analyse the effects of *D. yangi* or *Lipothymus* sp. on seed and pollinator production. Seeds or pollinators were dependent variables, *D. yangi* and *Lipothymus* sp. were independent variables, and the total number of female flowers was included as a covariate.

In the female floral phase, the fig emits specific volatile compounds that attract the fig wasps (van Noort *et al.*, 1989, Hossaert-McKey *et al.*, 1994). The fact that *Eupristina* sp., *D. yangi*, and *Lipothymus* sp. entered the figs on the same day suggests that they use the same chemical signal to find the receptive figs. Moreover, the two non-agaonid wasps must have identified by morphological and chemical traits whether *Eupristina* sp. has entered the fig. Since the two non-agaonid wasps actively select the figs and the ovaries visited by *Eupristina* sp., we assume an adaptive evolution between inquiline and the associated gallmaker. The significant negative correlation between the abundance of *Eupristina* sp. and the two non-agaonid species showed that the latter species killed or prevented the development of some individuals of the former species. As all the three wasps feed on the endosperm, competition for food – and possibly also for space – must be the mechanism(s) involved. Internally ovipositing non-agaonid wasps effectively pollinated *Ficus* and developed in the fig. This shows that the wasp and the fig form a mutualistic relationship, which, however, depends on the initial presence of the agaonid wasp. In spite of their detrimental influence on the agaonid, the internally ovipositing non-agaonid wasps contributed to the overall pollination success in passively pollinated *Ficus* species. Thus, our results show that the fig–fig wasp mutualism can result from different evolutionary lines.

The three species did not show competition or fighting behaviour when they entered figs, but when two foundresses of *D. yangi* entered a fig they fought fatally. In nature, figs apparently entered by only *D. yangi* (8%), only *Lipothymus* sp. (3%), or only *D. yangi* and *Lipothymus* sp. (2%) were observed. However, some foundresses of *Eupristina* sp. were observed to enter a fig and re-emerge. Similarly, at maturity 1% of figs had only *D. yangi* or *D. yangi* and *Lipothymus* sp. adults. In this case, the figs were probably entered by *Eupristina* sp. but all their offspring died before emergence.

In the controlled experiments, both *D. yangi* and *Lipothymus* sp. produced more offspring than *Eupristina* sp. when the agaonid and non-agaonid co-habited in the same fig. In a natural fig wasp community, 28% of adult fig wasps emerging from naturally colonized figs were *D. yangi* and 4% were *Lipothymus* sp. A significant negative correlation existed between the abundance of *Eupristina* sp. and either *D. yangi* or *Lipothymus* sp. However, *D. yangi* or *Lipothymus* sp. did not significantly affect seed production, either positively or negatively. *Diaziella yangi* colonizes more figs, but individual foundresses produce fewer offspring. In contrast, a foundress of *Lipothymus* sp. can produce more offspring, but fewer wasps are able to colonize figs. These differences indicate that the two non-agaonid wasps exploit the fig–wasp mutualism using different strategies, and *D yangi* has a higher fitness

than *Lipothymus* sp. because the former species exhibited both higher infestation rates and a bigger population.

A previous study reported that *Diaziella* and *Lipothymus* wasps entered *Conosycea* figs passively pollinated by *Waterstoniella* wasps at Brunei Darussalam (Jousselin *et al.*, 2001). Here we found that *Diaziella yangi* and *Lipothymus* sp. are associated with *Eupristina*-pollinated *Conosycea*. Although in our study species the pollinator was passive, most *Eupristina* are active pollinators. Moreover, in Borneo *Diaziella* species are yellowish like the *Waterstoniella* pollinators, whereas in Xishuangbanna they are black like the *Eupristina* pollinators (Rhett Harrison, personal communication). This wide distribution range points to an evolutionarily ancient and stable association and co-evolution of the internally ovipositing wasps and host fig. Geographical separation may have led to a change of the body colour. These findings suggest the co-evolutionary relationships between *Diaziella, Lipothymus*, agaonids, and their fig hosts are worthy of further study.

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