A fig crop pollinated by three or more species of agaonid fig wasps

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Species of fig trees (*Ficus*) and their fig wasp pollinators (Agaonidae) were traditionally thought to have a highly specific one-to-one relationship, but increasing numbers of exceptions to this pattern are emerging. Here we describe an exceptional situation, where four different agaonid species (*Alfonsiella brongersmai* Wiebes, *Alfonsiella natalensis* Wiebes, *Elisabethiella allotriozoonoide*s (Grandi) and *Alfonsiella longiscapa* Joseph) were recorded from a single host individual of *Ficus natalensis natalensis* Hochst. growing within its native range in Kibale Forest, Uganda. Germination studies confirmed that figs pollinated by at least three of the agaonid species contained viable seeds. Some of the agaonids are known to be associated with other *Ficus* species, raising the possibility that gene flow may be occurring between taxa in the *Ficus natalensis* species group. The figs also contained an exceptionally rich fauna of non-pollinating fig wasps (21 species), but there was no evidence that any non-pollinators were linked to figs pollinated by a particular agaonid.

Key words: Agaonidae, *Ficus,* host specificity, hybrid, parasitoid, pollination, Uganda.

INTRODUCTION

The relationship between fig trees (*Ficus* species, Moraceae) and their pollinator fig wasps (Hymenoptera: Chalcidoidea: Agaonidae) was for many years assumed to be strictly pair-wise, with each tree species pollinated by a single species of agaonid fig wasp that was associated with no other trees. Exceptions to this totally specific relationship have nonetheless accumulated over the years (Michaloud *et al.* 1996; Peng *et al.* 2008), and have multiplied thanks to the availability of molecular taxonomic techniques, which suggest that there may be many unrecognized cryptic species of fig wasps (Molbo *et al.* 2003; Erasmus *et al.* 2007). In addition to pollinator fig wasps there are also numerous species of non-pollinators belonging to other families of Chalcidoidea. These are mainly ovule gallers or parasitoids (Compton and van Noort 1992). Most also appear to be largely host tree specific (van Noort 1994; Jousselin *et al.* 2008). Although agaonids are responsible for pollination of the vast majority of the 800 or more species of fig trees, rare instances of 'non-pollinators' managing to pollinate have been recorded (Jousselin *et al.* 2001). Conversely, not all species of agaonid 'pollinators' actually pollinate their host plants, as neither the African *Ceratosolen galili* Wiebes, nor the Asian *Eupristina* sp. collect and transport pollen (Compton *et al.* 1991; Peng *et al.* 2008). The trees persist thanks to pollination by congeneric agaonids that share the same hosts.

The *Ficus natalensis* species group contains several African taxa with often poorly-defined species boundaries (Burrows & Burrows 2003; Erasmus *et al.* 2007) within the section *Galoglychia* (Rønsted *et al.* 2007). Extremely speciose fig wasp faunas, amongst the richest in the world, are a feature of the complex (Hawkins & Compton 1992), which may reflect an absence of specificity amongst some of their associated non-pollinating fig wasps. At least in southern Africa, the specificity of the plant–pollinator relationship is nonetheless usually retained, with individual trees typically being pollinated by a single species of fig wasp. Where more than one species of agaonid has been collected from what is regarded as a single taxon of tree, it has not been established whether more than one species was carrying out pollination that led to fertile seeds being produced (Boucek *et al.* 1981; Erasmus *et al.* 2007; Jousselin *et al.* 2008).

Here we describe a situation that contrasts strongly with the traditional view of the specificity of fig tree pollination, where an exceptionally species-rich fig wasp community, which included several agaonid species, was reared from a single crop of *F. natalensis natalensis* Hochst. We determined whether the agaonids were truly pollinators

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of the crop, and whether the high species richness of non-pollinating fig wasps was linked to the unusual number of pollinator species.

LOCALITY AND METHODS

Kibale National Park, with an area of 766 km^2, is located in western Uganda. The vegetation is transitional between lowland and montane rain forest and is classified as a mid-altitude, moist, evergreen forest with a canopy height typically between 20 and 30 m, but with some trees exceeding 55 m (Chapman *et al.* 1994; Mucunguzi, 2007; Struhsaker 1997; Wrangham *et al.* 1994). Mean annual rainfall totals 1734 mm, mean maximum temperature is 23.7 ° and mean minimum temperature is 15.5 ° (based on years 1990–2000) (Rode *et al.* 2006). This study was undertaken close to the Makerere University Biological Field Station in the Kanyawara area, which is at an elevation of 1500 m.

The range of *Ficus natalensis natalensis* (another subspecies, *leprieurii* (Miq.) C.C. Berg is found in Central and West Africa; and subspecies *graniticola* Burrows is found in southern Africa) encompasses altitudes up to 2200 m in wet and dry forest and woodland along the eastern side of Africa from Kenya inland to the Democratic Republic of Congo and south to KwaZulu-Natal in South Africa (Berg & Wiebes 1992). The species we studied at Kibale is one of at least two taxa that are referred to locally as *F. 'natalensis'.* It was readily distinguishable from the other form thanks to the larger size of its almost sessile figs (reaching a diameter of approximately 15 mm), which were yellow with prominent red spots when ripe. The tree was located at 0°33.960′N 30°21.989′E, near junction C23 on the Kibale forest path grid. Approximately 35 m tall, it was a large free-standing tree, with ripe fruit that were being consumed at the time by both birds and primates, most prominently by chimpanzees, *Pan troglodytes.*

Its crop size was estimated at over 50 000 figs. Fifty mature figs without exit holes were collected over a three-week period in August 2004 from amongst the many thousands of figs that had been knocked to the ground by the chimpanzees and other fig-eaters. The figs were split open and placed individually in sealed plastic vials with paper lids, into which the wasps emerged and were later killed using ethyl acetate. The figs were then dissected to remove those fig wasps that had failed to emerge from their galls and those, mostly males, that had remained within the central fig cavity. Conspecific males and females were associated where possible, but in some genera where two or more congeneric species were present the sexes could not be associated with certainty. The counts assumed that figs contained only conspecific males and females and some may be slight underestimates of the true species richness if unassociated males were present.

Seeds from figs that contained adults of either a single agaonid species, or a combination of species, were selected for germination trials to confirm that they were viable. Plastic Petri dishes 9 cm in diameter were lined with moistened filter paper and kept at room temperatures, which reached over 30 °C at times. Apparently healthy seeds (full-sized and hard) were counted and a sub-sample (30 if available) from each fig was placed in each dish. They were checked for germination at regular intervals for 30 days, after which all the remaining seeds in the Petri dishes were dissected to determine if they appeared healthy.

RESULTS

Fig wasp community richness

The 50 figs produced a total of 6995 adult fig wasps (mean = 139.9 individuals per fig, S.E. ±5.8, range 66–241), belonging to 24 distinguishable species (Table 1). Only two species were found in more than half of the figs sampled, 11 species were present in less than 10 %, and six were only recorded from a single fig. The rarity of many of the species was reflected in the typically low numbers of species present inside individual figs (mean = 4.6, S.E. ±0.3, range 1–13), with most of the figs (68 %) containing between three and five species. Agaonidae and Sycoecinae females ('foundresses') enter the figs to oviposit, whereas those of other taxa lay their eggs from the outside, through the fig wall. The former group are likely to lay all their eggs in a single fig, or a small number of figs, whereas the latter can disperse their eggs across many figs. This difference was reflected in the numbers of individuals present inside occupied figs, which was much higher in those species that enter the figs to oviposit (Table 1).

How many pollinators?

Four species of potential pollinators (agaonids) were recorded, three commonly and one from just a single fig (Table 1). Around half (28) of the figs

Table 1. The 24 species of fig wasps reared from a 50-fig sample from one crop of *Ficus natalensis natalensis* in Kibale Forest, Uganda.

Species	Higher taxon	Abundance		
		Frequency (figs where present)	Individuals	Occupancy (mean per occupied fig)
Elisabethiella allotriozoonoides	Agaonidae	23	1568	68.2
Alfonsiella longiscapa	Agaonidae	20	1203	60.2
Alfonsiella natalensis	Agaonidae	30	1896	63.2
Alfonsiella brongersmai	Agaonidae	1	14	14.0
Crossogaster sp. indesc.	Sycoecinae	2	183	91.5
Crossogaster hilli	Sycoecinae	8	540	67.5
Philocaenus geminus	Sycoecinae	1	56	56.0
Philocaenus ugandensis	Sycoecinae	14	1079	77.1
Philotrypesis sp. 1	Sycoryctinae	1	2	2.0
Philotrypesis sp. 2	Sycoryctinae	25	142	5.7
Watshamiella sp. 1	Sycoryctinae	11	23	2.1
Watshamiella sp. 2	Sycoryctinae	1	2	2.0
Sycoscapter sp. 1	Sycoryctinae	15	45	3.0
Sycoscapter sp. 2	Sycoryctinae	16	90	5.6
Sycoscapter sp. 3	Sycoryctinae	11	50	4.5
Sycophila sp. 1	Eurytomidae	1	2	2.0
Sycophila sp. 2	Eurytomidae	1	2	2.0
Sycophila sp. 3	Eurytomidae	3	4	1.3
Eurytoma sp.	Eurytomidae	2	2	1.0
Otitesella sp. 1	Otitesellinae	12	23	1.9
Otitesella sp. 2	Otitesellinae	16	48	3.0
Epichrysomallinae sp. 1	Epichrysomallinae	4	4	1.0
Epichrysomallinae sp. 2	Epichrysomallinae	3	5	1.7
Epichrysomallinae sp. 3	Epichrysomallinae	7	12	1.7

contained a single agaonid species, 19 had one or other of the three possible combination of pairs of agaonids, while two figs contained all three of the common species. The remaining fig was the only one containing *Alfonsiella brongersmai* Wiebes, which it shared with *Alfonsiella natalensis* Wiebes. The latter species was the only pollinator in 50 % of the figs where it was present, whereas the other two species were less frequently the sole potential pollinators (*Elisabethiella allotriozoonoide*s (Grandi), 26 %; *Alfonsiella longiscapa* Joseph, 35 %).

The germination trials included seeds from figs that had contained only one of the three more common species and figs containing the three combinations of pairs of species (Table 2: the single fig containing *A. brongersmai* was unsuitable for the trials because of a problem with mould). Most of the figs contained large numbers of apparently healthy seeds (Table 2; Fig. 1). Comparisons of overall germination rates between figs with different species of foundress detected no difference between *E. allotriozoonoides* and *A. natalensis,* but both had a higher proportion of apparently healthy seeds germinating than figs entered by *A. longiscapa* (2 × 2 Chi square tests with Yates' correction, both $P < 0.001$). The only two figs with no evidence of viable seeds were among those entered by *A. longiscapa,* although some figs entered by this species also produced large numbers of seeds. Seed germination rates varied widely between individual figs entered by the two *Alfonsiella* species (Fishers exact test, $P < 0.001$), but were consistent amongst figs entered by *E. allotriozoonoides* (Table 2; Fig. 2). Figs that had been entered by two different pollinator species contained about the same number of apparently healthy seeds as those entered by a single foundress. Caution is needed when interpreting the germination rates because some seeds that did not germinate within the 30-day period still appeared to be healthy and potentially capable of germinating at a later date, but the overall picture is of all three

Table 2. Germination trials with *Ficus natalensis natalensis* seeds from figs that contained different agaonid species. Trials 3 and 8 were based on only 22 and 7 seeds respectively. Other trials were based on 30 seeds.

Trial	Pollinator(s)	Apparently healthy seeds	Germination rates (%)	Estimated viable seed content
	E. allotriozoonoides			
1		108	66.7	72
2		108	76.7	83
3		22	54.5	12
4		181	66.7	121
5		63	56.7	36
	A. longiscapa			
6		46	0.0	0
7		106	10.0	11
8		7	0.0	0
9		99	86.7	86
10		164	46.7	76
	A. natalensis			
11		192	73.3	141
12		160	90.0	144
13		156	90.0	140
14		46	20.0	9
	E. allotriozoonoides + *A. longiscapa*			
15		68	56.7	38
	E. allotriozoonoides + *A. natalensis*			
16		86	53.3	46
17		118	43.3	51
18		163	46.7	76
	A. natalensis + *A. longiscapa*			
19		151	50.0	75
20		129	0.0	0

species being capable of pollinating the figs, and that between-fig variation in seed number and germination rates was more important than any between-pollinator effects.

Does pollinator diversity influence non-pollinator community structure?

All 50 figs contained representatives of at least one species of confirmed pollinator. There was no detectable influence of pollinator species on the presence or absence of non-pollinators as all the more common non-pollinators were found in figs pollinated by all three agaonids (Table 3). Some rare non-pollinator species were nonetheless recorded only from figs pollinated by a single species of agaonid, and more extensive sampling in the future may find that they are specifically associated with one or other agaonid.

DISCUSSION

The expectation, held for many years, that each species of fig tree is pollinated by a single species of agaonid fig wasp is giving way to a realization that the true situation is more complex. Although the one-to-one relationship still seems to hold for many species pairs, only a small number of fig tree species have been sampled repeatedly and throughout their range, or subjected to molecular techniques. Consequently, the number of species that are found to be routinely pollinated by more than one agaonid will inevitably increase. The one-to-one relationship also breaks down with one southern African fig wasp that apparently pollinates two different species of fig trees (Erasmus *et al.* 2007).

The association of four different species of

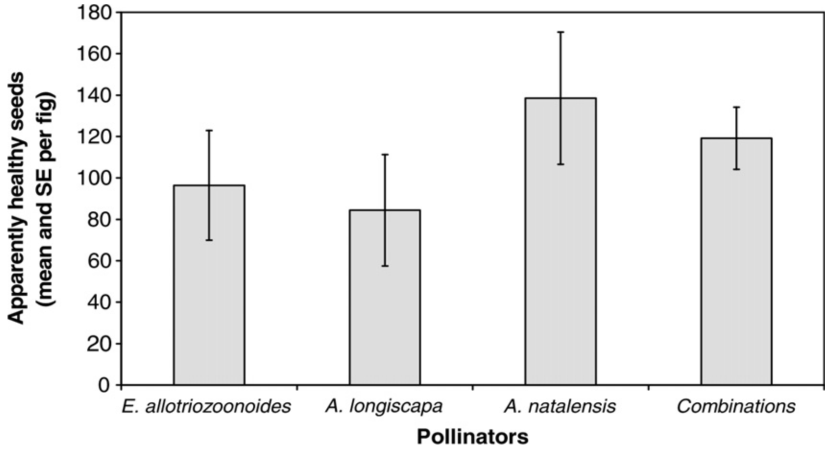

Fig. 1. The numbers of apparently healthy seeds present in figs of *Ficus natalensis natalensis* entered by different agaonid species, or combinations of species.

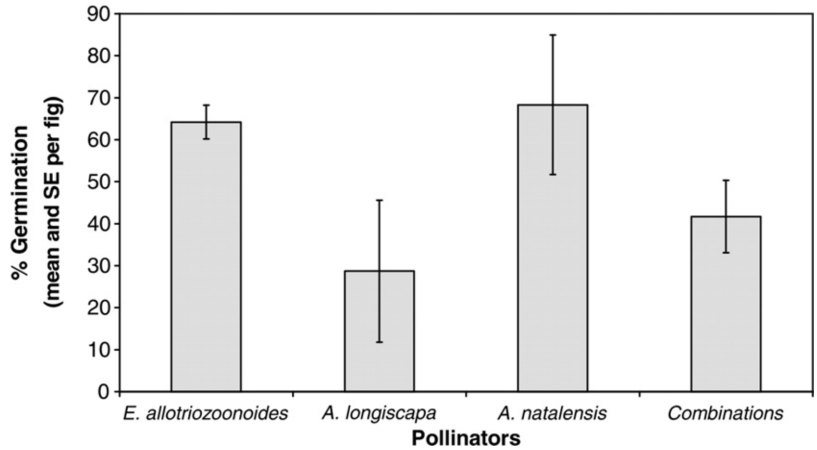

Fig. 2. Seed germination rates amongst *Ficus natalensis natalensis* figs entered by females of three different species of agaonids.

agaonids with a single *Ficus* crop has not been reported previously. Furthermore, the germination trials established that the three more abundant agaonid species, at least, were genuine pollinators of the tree. Pollination of figs is either passive, involving pollen transported fortuitously on the bodies of the insects, or a more pollen-efficient process involving the active collection and eventual dispersal of the pollen by the wasps. *Elisabethiella* and *Alfonsiella* species possess thoracic pollen pockets (Berg & Wiebes, 1992), which are adaptations for active pollination. *Ficus* species adapted for active pollination, such as *F. natalensis* and its relatives, produce relatively small amounts of pollen (Kjellberg *et al.* 2001) and would not be pollinated effectively via accidental transfer and so would not produce the large numbers of seeds present in the figs. The three common agaonids had therefore actively dispersed the pollen they had carried into the figs. Clearly all four species were also capable of reproducing successfully inside the figs.

The host ranges of the four agaonids we reared from the figs of *F. n. natalensis* are still poorly understood (Berg & Wiebes 1992; Erasmus *et al.* 2007; Jousselin *et al*, 2008). *Alfonsiella natalensis* was the most widespread and abundant of the four and the figs it had pollinated contained large numbers of seeds. It is only recorded from East Africa, with *F. n. natalensis* recorded as its host (Erasmus *et al.* 2007). *Elisabethiella allotriozoonoides* was almost as abundant as *A. natalensis* in the figs.

Table 3. The co-occurrence of non-pollinator and pollinator fig wasp species in figs of *Ficus natalensis natalensis.* Only figs containing a single species of agaonid are included. '0' = absent, '1' = present.

Non-pollinators	Pollinators		
Species	*Elisabethiella allotriozoonoides* (6 figs)	*Alfonsiella longiscapa* (13 figs)	*Alfonsiella natalensis* (7 figs)
Crossogaster sp. indesc.	0	1	0
Crossogaster hilli	1	0	1
Philocaenus geminus	0	1	0
Philocaenus ugandensis	1	1	1
Philotrypesis 1	0	0	1
Philotrypesis 2	1	1	1
Watshamiella 1	1	1	1
Watshamiella 2	0	0	0
Sycoscapter 1	1	1	1
Sycoscapter 2	1	1	1
Sycoscapter 3	0	1	1
Sycophila 1	0	0	1
Sycophila 2	0	0	0
Sycophila 3	0	1	1
Eurytoma sp.	0	0	0
Otitesella 1	1	1	1
Otitesella 2	1	1	1
Epichrysomallinae 1	1	0	1
Epichrysomallinae 2	1	1	0
Epichrysomallinae 3	1	1	1
Total	11	13	14

It too has only been recorded previously from the *F. natalensis* species group (unfortunately the actual host species was not recorded), and appears to be restricted to East Africa (Berg & Wiebes, 1992). *Alfonsiella longiscapa* has a wider distribution, extending from West Africa to Kenya and South Africa. It has been recorded previously from *F. n. natalen*sis in southern Africa, as well as from a related species (*F. burkei,* in Zambia, Boucek *et al.* 1981) and from *F. natalensis leprieurii* in West Africa (Erasmus *et al.* 2007). Some of the *F. n. natalensis* figs it entered produced no seeds, whereas seeds were abundant in some of the other figs. The significance of this is unclear. *A. brongersmai,* which has a similarly wide distribution across Africa, has also been reared from the figs of *F. burkei* and another closely related fig tree, *F. petersii* (Boucek *et al.* 1981).

At least five species of agaonids have now been recorded from the figs of *F. 'natalensis'* – those recorded here, plus *Elisabethiella socotrensis* (Erasmus *et al.* 2007). Because of the taxonomic difficulties associated with the *F. natalensis* species group (it is not clear whether *F. natalensis* will prove to be a single species or not) it was previously unclear whether the exceptional number of agaonids associated with *F. natalensis* was a reflection of (1) several closely related fig tree species, which we could not readily distinguish, each with their own host-specific pollinator, (2) of several fig wasps all associated only with one species of fig tree, (3) a more complex situation, with several non-host-specific agaonids utilizing more than one host plant or (4) a mixture of (2) and (3), with some host-specific agaonids utilizing *F. natalensis,* together with other pollinator species that have wider host ranges. Our results clearly do not support the first scenario, and given the wide host ranges of some of the agaonids, the second scenario also seems untenable.

Conversely, *A. natalensis* and *E. allotriozoonoides* have both only been recorded from *F. natalensis,* and may prove to be host-specific, if *F. natalensis* turns out to be a single species.

It may not be accidental that the first recorded instance of so many agaonids pollinating a single crop has come from Kibale, as this area has seen the expansion and contraction of savanna and forest habitats over extended periods, both as a result of climate change and through human interventions (Chapman *et al.* 2005). Such changes are likely to bring generate novel combinations of fig species within plant communities, increasing the chances of pollinator 'mistakes'. If any of the agaonids that pollinated our focal tree had developed as larvae in figs of other species of *Ficus* then any seeds produced would be hybrids. This is particularly likely for figs pollinated by *A. longiscapa,* given its wide host range. Increasing numbers of hybrid fig plants are being detected in natural habitats using molecular techniques (Parrish *et al.* 2003) and hybrids can often be generated after fig wasps are introduced into atypical host figs (S.G. Compton, pers. obs.). The figs pollinated by *A. natalensis, E. allotriozoonoides* and *A. longiscapa* were all capable of producing large numbers of seeds that germinated readily. Small numbers of seeds from figs pollinated by each species were also grown at the University of Leeds Experimental Gardens in the United Kingdom and produced consistently healthy plants. These may or may not have included hybrid individuals, but it is clear that with so many pollinators, some of which are known to be also associated with other species of fig trees, there is an increased probability of hybridization and potential introgression between *F. natalensis* and closely related species.

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