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Complementary fruiting phenologies facilitate sharing of one pollinator fig wasp by two fig trees

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Abstract

Aims

Most pollinator fig wasps are host plant specific, with each species only breeding in the figs of one fig tree species, but increasing numbers of species are known to be pollinated by more than one fig wasp, and in rare instances host switching can result in *Ficus* species sharing pollinators. In this study, we examined factors facilitating observed host switching at Xishuangbanna in Southwestern (SW) China, where *Ficus squamosa* is at the northern edge of its range and lacks the fig wasps that pollinate it elsewhere, and its figs are colonized by a *Ceratosolen* pollinator that routinely breeds in figs of *F. heterostyla*.

Methods

We recorded the habitat preferences of *F. squamosa* and *F. heterostyla* at Xishuangbanna, and compared characteristics such as fig size, location and colour at receptive phase. Furthermore, the vegetative and reproductive phenologies in the populations of *F. squamosa* and *F. heterostyla* were recorded weekly at Xishuangbanna Tropical Botanical Garden for 1 year.

Important Findings

Ficus squamosa is a shrub found near fast-flowing rivers, *F. heterostyla* is a small tree of disturbed forest edges. Although preferring different habitats, they can be found growing close together. Both species have figs located at or near ground level, but they differ in size when pollinated. Fig production in *F. squamosa* was concentrated in the colder months. *F. heterostyla* produced more figs in summer but had some throughout the year. The absence of its normal pollinators, in combination with similarly located figs and partially complementary fruiting patterns appear to have facilitated colonization of *F. squamosa* by the routine pollinator of *F. heterostyla*. The figs probably also share similar attractant volatiles. This host switching suggests one mechanism whereby fig trees can acquire new pollinators and emphasizes the likely significance of edges of ranges in the genesis of novel fig tree–fig wasp relationships.

Keywords: Agaonidae, edge of range, *Ficus*, host specificity, host switching

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INTRODUCTION

Plants often exhibit reduced reproductive success towards the edge of their ranges (Jump and Woodward 2003; Jump *et al.* 2006) and in more seasonal environments (Muñoz and Arroyo 2006; Totland 2001), where the timing of reproduction becomes more critical (Kozłowski 1992). Plants that require specific pollinators may be particularly liable to show declines in reproductive success at range margins (Xiong *et al.* 2015). The relationship between fig trees (*Ficus* spp.) and their fig wasp pollinators (Agaonidae) is usually typified as being strictly obligate, with each *Ficus* species pollinated by one host plant-specific agaonid species that enters the figs in order to lay its eggs (Galil 1973; Janzen 1979). The one pollinator to one fig tree pattern described in earlier publications has now been replaced by a realization that fig trees often support two or more host-specific pollinator species (Chen *et al.* 2012; Moe *et al.* 2011; Molbo *et al.* 2003; Rasplus 1996; Yang *et al.* 2015; Zhang *et al.* 2004). Rasplus (1996) estimated that 20% of African fig tree species may support more than one species of pollinator and additional sampling can only have increased this figure. Often the different pollinators are largely allopatric, occupying different geographical areas or habitats within their host plant's range (Chen *et al.* 2012; Kerdelhue *et al.* 1997; Michaloud *et al.* 1996), but individual trees can also produce crops that are serviced by more than one pollinator species (Compton *et al.* 2009).

Fig wasps sometimes enter figs of atypical host species. This occurs more commonly if the trees concerned have been planted outside their native range and consequently do not have their typical pollinators available to them (Ware and Compton 1990). The wasps are often unable to reproduce successfully in these atypical hosts, but adult offspring (and hybrid seed) can be generated. Examples where two fig tree species routinely share the same pollinators have been recorded less frequently and such pollinator sharing clearly has implications for the reproductive isolation of the fig trees that share pollinators, if their populations are sympatric. An example of two largely geographically isolated fig trees sharing the same pollinator is provided by *Ellsabethiella socotrensis*, which pollinates *Ficus vasta* in Ethiopia and Saudi Arabia, and *F. wakefieldii* in Kenya and Zambia (Rasplus 1996), but in southern Africa this species also pollinates additional *Ficus* species, that can be growing together (Cornille *et al.* 2012). *F. auriculata* and *F. oligodon* are sympatric trees that share two pollinator species in China (Yang *et al.* 2012; F. Kjellberg, personal communication). Factors favouring agaonid colonization of more than one fig tree host are unclear (Yang *et al.* 2012), but host specificity results from a combination of tree-specific volatile compounds that attract a tree's pollinators to receptive figs, surface cues on the figs, a head shape and size that permits entry into the figs and an ovipositor of appropriate length (Liu *et al.* 2013; Nefdt and Compton 1996; Proffit and Johnson 2009; van Noort *et al.* 1989; Wang *et al.* 2013). These suggest that sharing of pollinators is more likely to develop when two *Ficus* species have figs that share similar physical characteristics and the volatile profiles that allow pollinator entry and oviposition.

Low rates of pollinator sharing appear to be the norm even among closely related sympatric fig trees (Moe *et al.* 2011). In SW China, *F. squamosa* is at the northern edge of its natural range and is sympatric with *F. heterostyla*. Locally, the two fig trees share an undescribed *Ceratosolen* pollinator (J.-Y. Rasplus, personal communication), despite belonging to different sections of *Ficus* subgenus *Sycomorus* (Berg and Corner 2005). The shared fig wasp is the only pollinator recorded for *F. heterostyla* locally, and has not been recorded outside the distribution of *F. heterostyla*, whereas *F. squamosa* is routinely pollinated by two other *Ceratosolen* species elsewhere (P Pothasin and SG Compton, unpublished data), suggesting a local extension of this pollinator's host range to include *F. squamosa*.

It is known that *Ficus* populations necessarily include some plants with figs throughout the year, which permits a continuous cycling of pollinators between trees (Bronstein *et al.* 1990; Patel 1996). Reproductive phenology often has small seasonal fluctuations near the equator, but shows a significant variation at Xishuangbanna at the northern margin of tropical SE Asia (Corlett 1987; Peng *et al.* 2010) where a phenological mismatch was found to result in the non-pollinating fig wasp *Apocryptophagus* sp. switching reproduction from male to female figs of *F. auriculata* (Peng *et al.* 2005). Females of the *Ceratosolen* species that routinely pollinates *F. heterostyla* are clearly a good physical match with the figs of *F. squamosa* at Xishuangbanna, because they are able to enter its figs and lay eggs there. We tested the hypothesis that host switching was being facilitated by similarities between the two species and addressed the following questions (i) Do the two plants grow together? (ii) Are their figs similar in size and location on the trees? and (iii) Is the seasonal development of their figs and leaves similar?

MATERIALS AND METHODS

Study site

Xishuangbanna Tropical Botanical Garden (XTBG) is located in Southwest China (21°55′N, 101°15′E, ~555 m a.s.l.) at the northern edge of the Asian tropics. The garden is within a tropical rainforest reserve that supports many *Ficus* species. Temperature and rainfall data collected for 40 years at the nearby Xishuangbanna Forest Ecology Station show that mean annual temperatures were 21.8°C, with means of 25.7°C in the hottest month (June) and 16.0°C in the coldest month (January). Average annual relative humidity was 85%, with 80–90% of the rainfall in the rainy season between May and October and 10–20% in the November to April dry season. Climatic variation during the study period is summarized in Fig. 1.

Study species

Ficus squamosa Roxburgh (subgenus *Sycomorus*, section *Sycocarpus*; Berg and Corner 2005) is a short dioecious shrub. Male plants have figs that support the development of pollinator larvae, female plants have figs that only contain seeds. The figs of both sexes are located in the leaf axils or on tuberculate branchlets arising from old stems. *F. squamosa* is typically found growing in or near fast-flowing streams and rivers. The mature female (seed-containing) figs are dispersed by water, rather than vertebrates (Berg and Corner 2005). It has a natural distribution that extends from Malaysia to southwestern China. Xishuangbanna is at its northern range limit, but it is locally abundant on the banks of major rivers. These plants are subject to flood events in the rainy season, with bank erosion and sediment burial, which limits regular access. Therefore, ~200 locally sourced individuals were transplanted

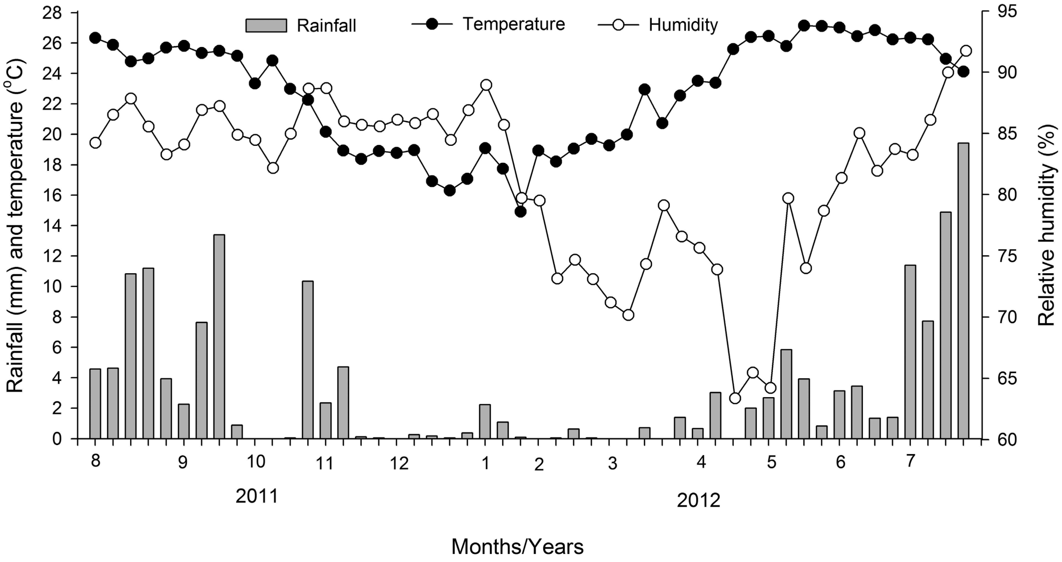

Figure 1: variation in temperature, rainfall and humidity at XTBG during the study period.

to sites within XTBG in 2008. The transplanted fig trees are ~500 m away from the natural riverine population.

Ficus heterostyla Merr. (subgenus *Sycomorus*, section *Hemicardia*; Berg and Corner 2005) is a small dioecious tree that grows to ~10 m. It is a forest species, distributed from southern Vietnam to Xishuangbanna in China. The figs are located on long stolons that can run along the ground or under the soil surface for several metres away from the trunk (flagelliflorous). The location of the figs suggests that they are dispersed mainly by ground-feeding vertebrates such as pigs (Shanahan *et al.* 2001).

Ficus squamosa and *F. heterostyla* occur naturally at XTBG, where they share an undescribed pollinating fig wasp *Ceratosolen* sp.1 (Fig. S1, see online supplementary material). It is the only pollinator recorded locally from the figs of *F. heterostyla*. A second unidentified pollinator is present rarely in the figs of *F. squamosa* at XTBG. It is not one of the species that routinely pollinates *F. squamosa* elsewhere in the plant's range and may represent a second switch between host trees (Fig. S1 and S2, see online supplementary material).

Tree distribution at XTBG

Surveys over several years have located the distributions of the *Ficus* species at XTBG. We compared the habitats and distributions of the two focal species, and how close together they were growing.

Fig characteristics

When figs become receptive (B phase *sensu* Galil and Eisikowich 1968) they release volatile blends that are usually attractive only to that tree's specific pollinator (van Noort *et al.* 1989). The sizes of B phase figs were compared based on measurements of 18 female and 19 male figs of *F. heterostyla*, and 10 female and 15 male figs of *F. squamosa*. Only one or two figs were collected from each *F. squamosa* tree, because of its very small crop sizes. The *F. heterostyla* figs were obtained from seven female and eight male trees. Colours were noted and measurements taken using digital calipers of fig length (from the pedicel to ostiole), and width (the maximum diameter at right angles to this axis). To compensate for minor irregularities in shape, two measurements of the diameters were taken and a mid value was used.

Vegetative and reproductive phenologies

The seasonal production of new leaves and new figs is linked in some *Ficus* species (Peng *et al.* 2010). We recorded the leaf and flowering phenologies of 19 female and 32 male transplanted *F. squamosa*, and 18 female and 19 male *F. heterostyla* weekly at XTBG from 4 August 2011 to 27 July 2012. The leaves on each tree were assigned to one of the following character states: new leaves emerging from buds, growing leaves, mature leaves and senescing leaves. The developmental stages of all the figs on each *F. squamosa* were recorded, together with their developmental stages, whereas on each *F. heterostyla* around 30 figs (if present) were examined. The concealed locations of its figs meant that accurate crop size estimates were not possible. Five fig developmental phases were distinguished (based on Galil and Eisikowich 1968): A (pre-female phase), B (receptive or female phase, when figs are entered and pollinated), C (inter-floral phase, when seeds and wasp offspring are developing), D (male phase, when the next generation of wasps emerges from male figs, this phase is absent from female figs) and E (post-floral phase, after the figs have been vacated and female figs become attractive to seed dispersers). B phase figs were distinguished by the presence of open ostiolar bracts, and D phase figs by the presence of exit holes in male figs. Changes in the colour and softness in female figs indicated the equivalent start to E phase in female figs.

To check if the reproductive phenologies of the transplanted and naturally growing *F. squamosa* were similar, two riverine populations of 15 and ~100 trees were investigated at times when they were accessible, in November 2011, March and April 2012, and June 2013. The smaller population was 500 m away from the transplanted trees, and the larger was ~5 km away.

Data analysis

Mann–Whitney and Kruskal–Wallis tests were used to compare between-species and between-sex differences in the sizes of B phase figs. Mann–Whitney tests were also used to the numbers of figs on female and male *F. squamosa*. Spearman correlations analyse the relationship between leaf initiation and climatic data, and between fig and leaf initiation. The analyses were conducted in SPSS 16.0.

RESULTS

Habitat preferences

Ficus heterostyla individuals were mainly located at the edges of disturbed forest areas, and roadsides where there was only partial canopy cover. The riverside conditions where *F. squamosa* grows naturally were more open, but sometimes close to forest edges. The minimum distance we recorded between individuals of the two species was 20 m.

Fig size and colour

Receptive figs of the two species were dark green, had scattered surface hairs and had a roughly similar globular shape. Receptive female figs of both species had a significantly larger diameter than receptive male figs of their respective species (Table 1). There was also significant within-sex variation between trees in the size of receptive *F. heterostyla* figs (females: Mann-Whitney [M-W], $Z = -3.800$, $P < 0.001$ for diameter and $Z = -3.047$, $P = 0.002$ for length; males: Kruskal-Wallis, $\chi^2 = 44.492$, and $\chi^2 = 40.157$, respectively, both $P < 0.001$). Too few figs per plant were present to allow a similar assessment for *F. squamosa.*

Receptive female *F. squamosa* figs were broader and longer than equivalent female *F. heterostyla* figs (M-W, $Z = -5.182$, $P < 0.001$ and $Z = -5.183$, $P < 0.01$, respectively). Receptive male figs of *F. squamosa* were also larger than those of *F. heterostyla* ($Z = -5.706$ for diameter and $Z = -6.018$ for length, both $P < 0.001$).

Phenology

Mature green leaves formed 91% (*F. squamosa*) and 87% (*F. heterostyla*) of the total leaf states recorded during the 1-year recording period (Fig. 2). There was little seasonal variation in the leaf states on the *F. squamosa* trees, with small quantities of new and senescing leaves present more or less continuously and no differences between the sexes (Fig. 2). In contrast, the leaf phenology of *F. heterostyla* showed marked seasonal variation, with a major leaf drop usually in the spring dry period from April to May, when 5 of the 37 sampled trees had shed all their leaves. This was followed by a flush of new leaves that peaked in June. New leaf initiation in *F. heterostyla* was concentrated in the warm wet season and was positively correlated with weekly rainfall during the survey period (female: $r = 0.501$, $P < 0.01$; male: $r = 0.538$, $P < 0.001$) and mean temperatures (female: $r = 0.841$, $P < 0.001$; male: $r = 0.744$, $P < 0.001$). No significant correlations with climatic variables were present in *F. squamosa*. Fig and leaf initiation on *F. heterostyla* were highly correlated ($r = 0.203$, $P < 0.001$), but there was no correlation between fig initiation and flushes of new leaves on *F. squamosa* bushes ($r = 0.014$, $P = 0.436$).

Fig development was recorded on 51 *F. squamosa* and 37 *F. heterostyla* trees. Long development times meant there were many multiple observations of the same figs. *F. squamosa* had few figs present at any one time with maxima of 11 figs on male plants and 7 on female plants (Fig. 3). There was no difference in the maximum numbers of figs present at any one time on male and female plants (M-W, $Z = -1.488$, $P = 0.137$). Although precise counts were not possible because of their location, *F. heterostyla* produced more figs, with 30 or more regularly recorded from trees of both sexes.

Fig production in the transplanted *F. squamosa* was concentrated in the colder, drier months of the year, and they were entirely absent from male trees for almost 6 months. Most female trees also only had figs for ~6 months of the year (Fig. 4). We could not gain close access to the natural riverine populations of *F. squamosa* throughout the year, but the available data shows a similar pattern to that of the transplants, with figs only recorded on the trees in the cool (November) and dry (March and April) seasons. During the rainy season, flood waters inundated many of the plants and although no figs were visible, some may have survived under the water. The breaks in fig production at XTBG are not typical of the plant further south, where figs are present all year (P. Pothasin, personal communication).

The development of *F. squamosa* figs was slow, reflecting the relatively cool temperatures at the times when figs were present, and resulted in largely synchronized crops on individual trees and across the population as a whole, especially during the earlier stages of fig development (Fig. 5). A maximum of two generations of pollinators were able to complete their development during the relatively short period when figs were present on the male trees and some female figs were pollinated earlier than any recorded emergence of fig wasps from male figs of this species (Fig. 6).

The fruiting phenology of *F. heterostyla* was different to that of *F. squamosa*. Four of the 18 female trees and three of the 19 male trees had figs present throughout the year, but there was also a well-defined summer peak in the number of trees that were bearing figs. Male and female trees had broadly similar fruiting phenologies, with the number of trees with figs increasing in summer (Fig. 4), but the proportion of young, recently initiated figs peaked ~2 months earlier in males than in females (Fig. 5).

Table 1: the diameter and length of male and female figs of *Ficus squamosa* and *F. heterostyla* at the developmental stage when they are entered by pollinators (B phase)

	F. squamosa			*F. heterostyla*		
Fig sizes	Female (*n* = 10 figs) Mean ± SE	Male (*n* = 15 figs) Mean ± SE	M-W *Z* (*P*)	Female (*n* = 94 figs) Mean ± SE	Male (n = 70 figs) Mean ± SE	M-W *Z* (*P*)
Diameter (mm)	18.92 ± 0.92	12.80 ± 0.32	−3.938 (<0.001)	10.17 ± 0.13	9.45 ± 0.15	−3.876 (<0.001)
Length (mm)	19.83 ± 1.03	12.66 ± 0.41	−3.994 (<0.001)	8.27 ± 0.11	8.31 ± 0.13	−0.429 (0.668)

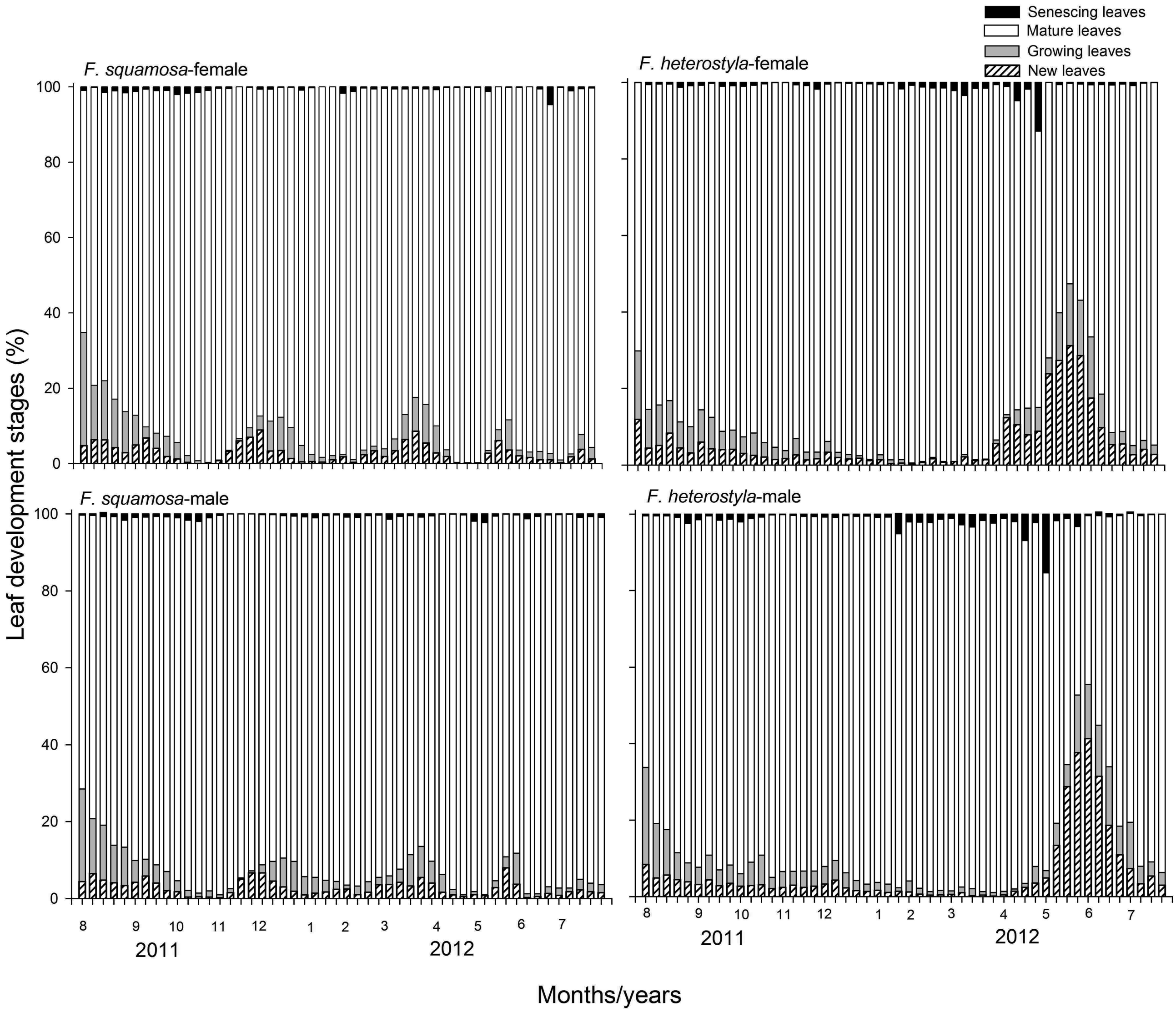

Figure 2: leaf phenology of *Ficus squamosa* and *F. heterostyla* at XTBG.

Timing of fig wasp emergence and figs available for entry

Fig wasps emerging from D phase figs disperse in search of receptive figs where they can lay their eggs. The male trees of *F. squamosa* only had D phase figs present between March to May (with very few figs releasing wasps before late April), whereas their B phase figs were present between January and April (Fig. 6). This meant that very few fig wasps emerging from the male figs had conspecific receptive figs to enter. Reflecting this, the next generation of pollinators released by the plants was very limited in size. B phase figs on female *F. squamosa* trees were concentrated between March and May, with small numbers also present a few months earlier (Fig. 6). Despite the almost total absence

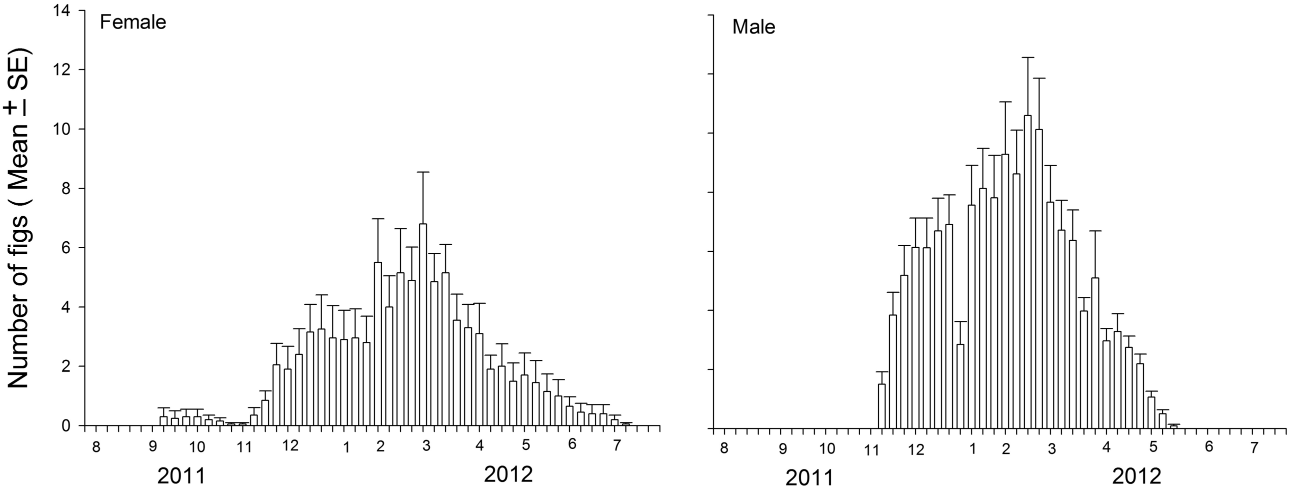

Figure 3: annual variation in crop sizes on male and female *Ficus squamosa* at XTBG.

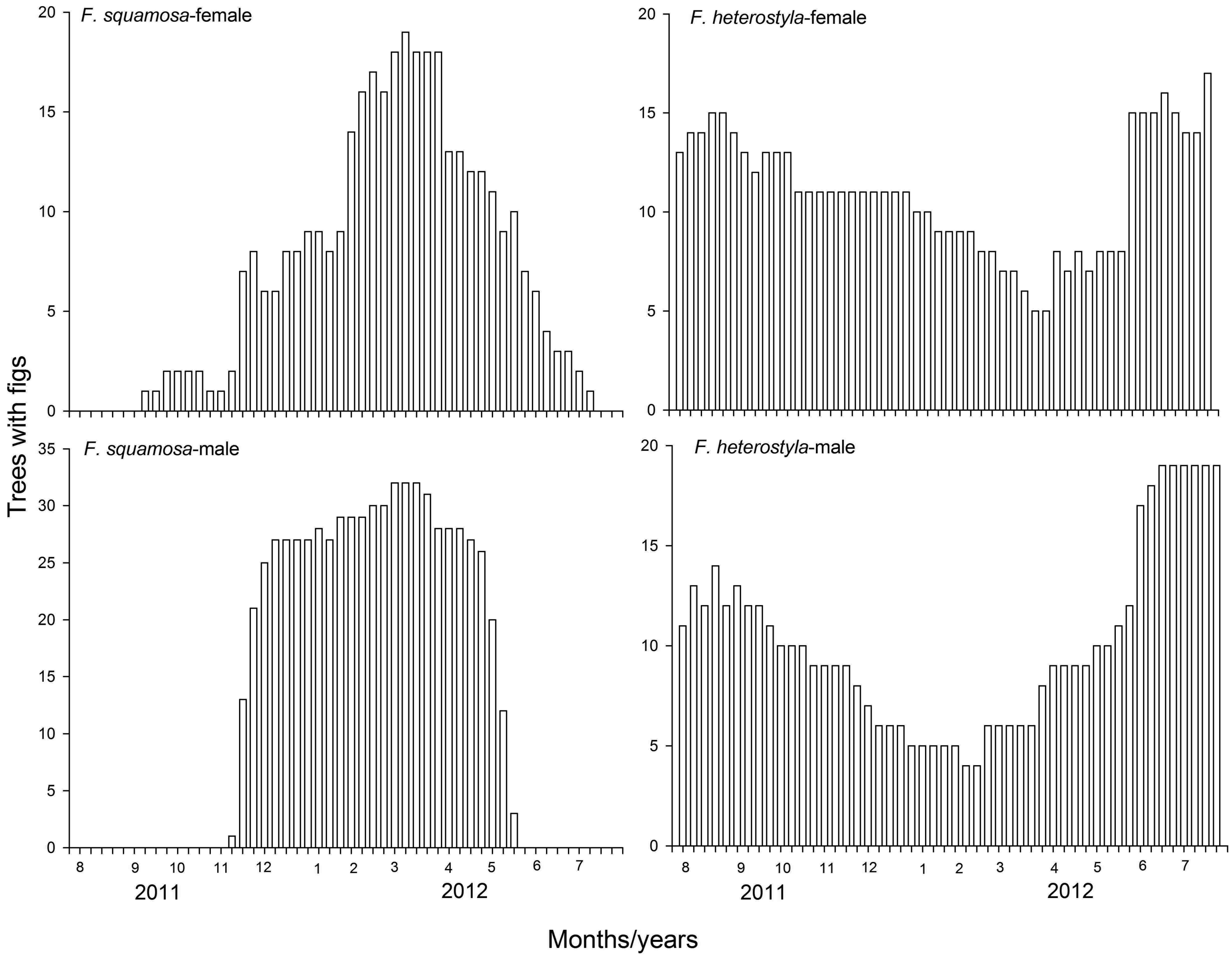

Figure 4: annual variation in the numbers of *Ficus squamosa* and *F. heterostyla* with figs at XTBG.

of pollinators emerging from local *F. squamosa* before March, all the B phase male and female figs were entered by fig wasps (Fig. 6).

Five female and four male trees produced figs that aborted at an early stage, before they became receptive to pollinators. All the female *F. squamosa* figs present in September to

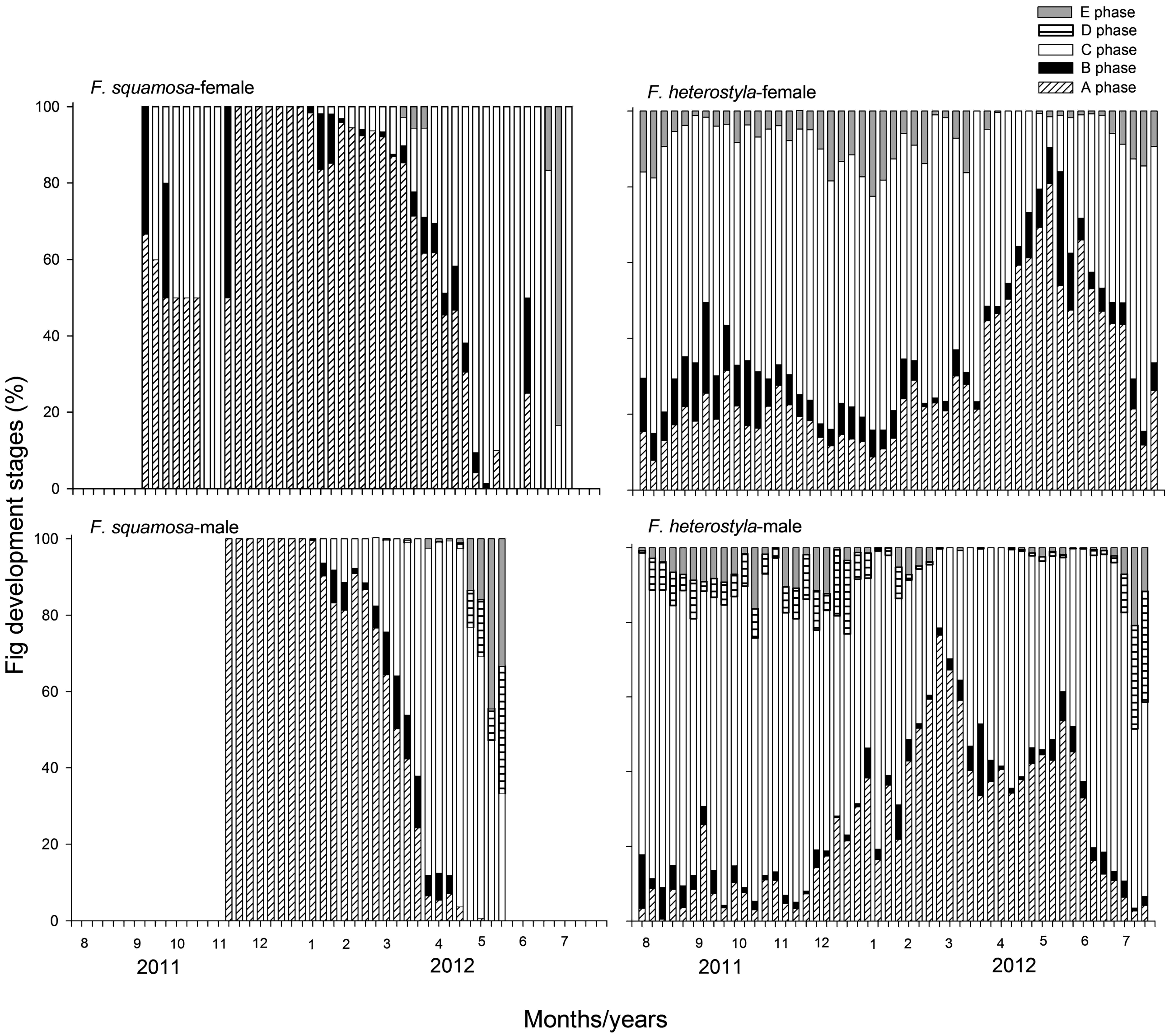

Figure 5: annual variation in the developmental stages of figs of *Ficus squamosa* and *F. heterostyla* at XTBG.

November 2011 aborted. Abortions were also more frequent in January to February than in the later months of 2012. These later stage aborted figs contained numerous pollinator females (mean ± SE = 3.40 ± 1.05 fig wasps within the ostioles and 3.85 ± 0.88 within the fig cavities (n = 20 figs). Two aborted male figs were also examined, both of which had also been entered by pollinator females. Therefore, a shortage of pollinators was not the reason for the abortions among figs that reached B phase.

In contrast to *F. squamosa*, B phase figs of female *F. heterostyla* were present throughout the year (Fig. 6). B phase and D phase figs overlapped on many of the male trees, allowing the cycling of pollinator populations on the same trees, and some D phase figs were recorded every month of the year (Fig. 6). Consequently, fig wasps were emerging from *F. heterostyla* figs throughout the period when receptive *F. squamosa* figs were present, but none of its pollinators were being released locally.

DISCUSSION

Adult female fig wasps have a very short lifespan of ~1 day (Kjellberg *et al.* 1988). Receptive figs must therefore be available at the same time as pollinators are released in order to maintain local populations of the insects, and the fruiting phenologies of *Ficus* species reflect this (Patel 1996, Patel and Hossaert-McKey 2000; Peng *et al.* 2010; Suleman *et al.* 2011). Their phenologies are nonetheless responsive to climatic conditions (Compton 1993) and the highly seasonal climate in southwestern China appears to generate phenological patterns in *F. squamosa* growing at the northern edge of its range that preclude the maintenance of populations of its associated fig wasps.

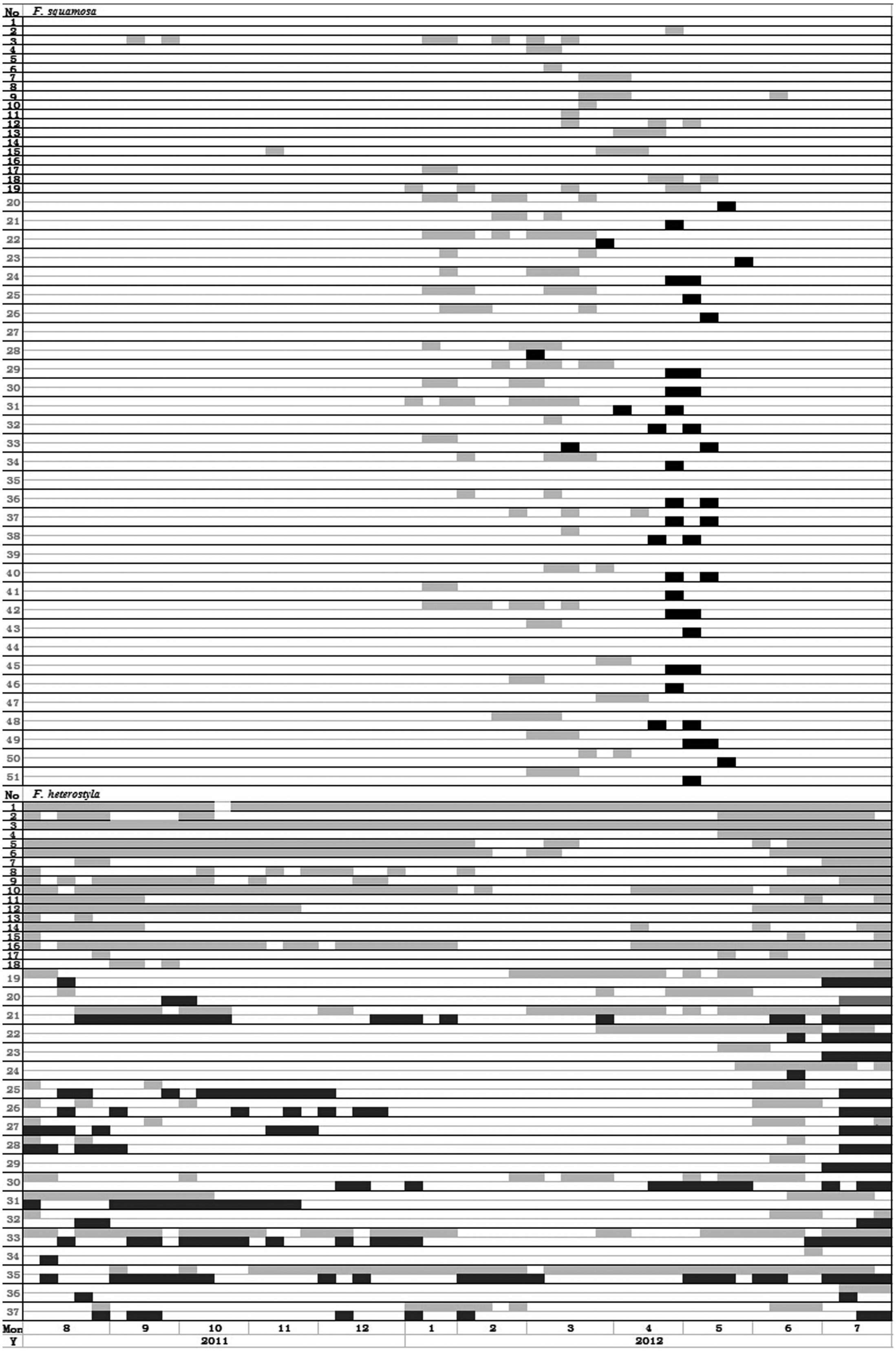

Figure 6: periods when B phase figs (receptive for pollinators, grey fragments) and D phase figs (when fig wasps are being released, black fragments) of *Ficus squamosa* and *F. heterostyla* were present at XTBG. Narrow strips represent female trees and wide strips male trees. All the B phase figs of *F. squamosa* were entered by fig wasps.

Fig production in *F. squamosa* was concentrated in the cold and dry months of the year. A single annual generation of pollinators emerged from *F. squamosa* male figs at a time when some conspecific female figs were receptive, so these figs could be entered by fig wasps carrying *F. squamosa* pollen and seed set could develop as normal. These seeds can be the source of new individuals into the *F. squamosa* populations around XTBG. However, the species appears unable to cycle, and thereby maintain continuously, independent pollinator populations throughout the year because of the breaks in male fig production. This is likely to be the reason that the pollinators associated with *F. squamosa* towards the centre of its distribution are absent at XTBG. In their absence, the plant has recruited the services of the pollinator fig wasp associated with *F. heterostyla* (and also very small numbers of a second pollinator species).

We examined factors that may have facilitated the recruitment by *F. squamosa* of the fig wasp that routinely pollinates *F. heterostyla*. Volatiles released from receptive figs are a key element in the host specificity of most fig wasps (Soler *et al.* 2012; van Noort *et al.* 1989), and the two species presumably share related volatile profiles. However, the two tree species are not extremely closely related and SW China has numerous other fig trees pollinated by different *Ceratosolen* species, so *F. heterostyla* was not the only potential source of pollinators. *F. heterostyla* and *F. squamosa* prefer different habitats, but small numbers of plants can be found growing only a few metres apart, so spatial separation of the species does not prevent dispersal of pollinators between the two. The colour and shape of the receptive figs of *F. squamosa* and *F. heterostyla* are similar, but they differ in size at the time they are entered by pollinators. Although fig surface characters can influence pollinator behaviour (Wang *et al.* 2013), the large size difference between receptive male and female figs of *F. squamosa* shows that the pollinator does not use cues associated with size when deciding which figs to enter. The size difference between receptive figs of the two *Ficus* species was clearly not a barrier to pollinator transfer.

The *Ceratosolen* that pollinates *F. heterostyla* has to search for figs that are located at ground level and are often partially covered with soil or vegetation debris. *F. squamosa* is a small bush and often has figs positioned close to the ground. If the pollinator of *F. heterostyla* concentrates its host searches close to the ground then this will have facilitated encounters with receptive *F. squamosa* figs that were waiting to be entered. This in itself is not sufficient to explain the switch in hosts between the two species, because there are other fig tree species at XTBG that also produce figs at or near ground level. Like most *Ficus* species, *F. heterostyla* at XTBG bears fruit year-round, but with a well-defined summer peak in the number of trees with figs. The two *Ficus* species showed partially complementary phenologies, insofar as male trees of *F. heterostyla* were regularly releasing pollinators at times when receptive figs of *F. squamosa* were available and ready to be pollinated, but no pollinators were being released from *F. squamosa* to service them. The results confirmed the hypothesis that the complementary flowering phenologies of two *Ficus* species facilitated host switching of the pollinators.

Taken together, our results show why it is possible for the routine pollinator of *F. heterostyla* to enter figs of *F. squamosa*, but they do not explain why it is this particular pollinator rather than other species, that has done so. A comparison of the volatiles emitted by receptive *F. squamosa* and *F. heterostyla* figs, investigations on phylogenetic and climatic constraints on flowering (Pei *et al.* 2015) and the molecular mechanisms of flowering (Li *et al.* 2015) may provide the answer. The entry of pollinators that carry *F. heterostyla* pollen into female figs of *F. squamosa* (and *vice versa*) could lead to hybrid offspring, and our preliminary experiments involving the experimental transfer of *Ceratosolen* into female figs has confirmed that hybrid seeds are produced, although in small numbers (GX Liu and YQ Peng, unpublished data). For the pollinator of *F. heterostyla*, female figs of both species are traps, but because this fig wasp can reproduce successfully inside the male figs of *F. squamosa*, they are providing additional resources for its reproduction. Thompson (1999) has emphasized the importance of a geographic perspective for studies of mutualistic systems. Host switching suggests one mechanism whereby fig trees can acquire multiple pollinators and emphasizes the likely significance of edges of ranges in the genesis of novel fig tree–fig wasp relationships.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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Conflict of interest statement. None declared.

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