A New Case of Ants Nesting within Branches of a Fig Tree: the Case of *Ficus subpisocarpa* in Taiwan

by

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ABSTRACT

Ficus is one of many plant genera involved in interactions with ants. The interaction is however little documented. We show here that ants, belonging mainly to the genus *Crematogaster*, nest in hollow internodes of young branches of *Ficus subpisocarpa*, a monoecious fig species studied in Taiwan. The ants feed on the mutualistic fig-pollinating wasps as well as on parasitic non-pollinating fig wasps. Nevertheless fig-wasps may not constitute a sufficient food source to ensure permanent presence of ants on the tree as the ants were observed to be frequently associated with hemipterans such as coccids and aphids. Fig wasps seem to constitute a reliable and sufficient food source on some dioecious *Ficus* species. On the contrary, in monoecious *Ficus* species, resident ants have always been observed to tend homopteran in addition to feeding on fig wasps. Frequent fruiting, prolonged fruit ripening period, ramiflory and rapid growth could constitute traits facilitating strong association based on fig-wasps' consumption of the monoecious *F. subpisocarpa* with ants. Despite these traits, ants were observed to tend hemipterans, and *F. subpisocarpa* does not seem to have evolved specialized morphological traits to facilitate the association.

Key words: ant-plant interaction, community ecology, Asian biodiversity, myrmecophytism, ant foraging.

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INTRODUCTION

A major challenge of ecology is the assessment of species' communities and the understanding of the determinants of their structure and organization (Fortuna & Bascompte 2006; Bascompte & Jordano 2007; Proffit *et al.* 2007; Bascompte 2009; Cavender-Bares *et al.* 2009; Ings *et al.* 2009; Vázquez *et al.* 2009). Various groups of insects have inspired the development of theories in community ecology. They have long been recognized as convenient models for testing hypotheses in this domain (Heil & McKey 2003). Among them, ants (Hymenoptera: Formicidae) can be central for such perspectives, as they often play a major role in interaction networks as predators (Lach *et al.* 2009), seed dispersers (Giladi 2006), pollinators (Rico-Gray & Oliveira 2007), mutualistic defenders of their host-plants (Heil & McKey 2003; Heil 2007) and exploiters of various mutualisms (Schatz *et al.* 2006, 2008). More specifically, ants have been widely studied for their interactions with plants. Ant-plant protection mutualisms have been reported in 100 plant genera and 40 ant genera, mainly in tropical regions (Davidson & McKey 1993; Speight *et al.* 2008). The high diversity of this type of interaction even within genus (Webber *et al.* 2007) is explained by easy development of mutualistic interactions. Indeed, the strong potential protection against herbivores provided by ant colonies may substantially increase plant fitness (Rosumek *et al.* 2009). Specialized ant-plant interactions have been used as ecological and evolutionary models to understand selective factors affecting plants (Heil & McKey 2003). Some of these specialized interactions have been shown to be structured by chemical mediation (Ranganathan & Borges 2009; Schatz *et al.* 2010) and support complex networks of plurispecific interactions involving herbivores, parasites, predators and secondary mutualists (Palmer *et al.* 2008; Schatz *et al.*, 2008, 2010; Blatrix *et al.* 2009; Goheen & Palmer 2010).

Among the numerous genera of plants associated with ants, the interaction between *Ficus* and ants has been poorly studied. *Ficus* is one of the 100 plant genera presenting what has been interpreted as structures specifically evolved to host ant nests (Speight *et al.* 2008), with only a single case hitherto reported for this genus (Maschwitz *et al.* 1996). Fig species are known for their obligate species-specific nursery pollination mutualisms with fig wasps (Janzen 1979; Kjellberg *et al.* 2005). Specificity is reinforced by a physical filter (matching

between pollinator head shape and ostiole structure; van Noort & Compton 1996) and chemical mediation (emission of volatile compounds responsible for pollinating wasp attraction by receptive figs; Grison *et al.* 1999; Proffit *et al.* 2007, 2008, Hossaert-McKey *et al.* 2010). *Ficus* are increasingly investigated for their role in supporting a complex network of interactions involving a community of species-specific parasitic chalcid wasps (regionally up to 25 parasitic species for a single *Ficus* species, Bouček *et al.* 1981), but also several species of ants, all of them capable of detecting and using chemical signals emitted by figs (Chen *et al.* 1999; Kjellberg *et al.* 2005; Proffit *et al.* 2007; Ranganathan *et al.* 2010; Schatz *et al.* 2008, 2010). Within that network, ants have been shown to severely reduce the prevalence of parasites and to be a structuring factor for various other insect species (other predators, herbivores, visitors) (Schatz & Hossaert-McKey 2003; Schatz *et al.* 2006, 2008, Wei *et al.* 2005). Ants have often been reported to be predators of fig wasps. They have also been observed to participate in fig-seed dispersal (Kaufmann *et al.* 1991; Roberts & Heithaus 1986; Laman 1995, 1996) and they are involved in ant-homopteran-fig tree tritrophic interactions (Compton & Robertson 1988, 1991; Dejean *et al.* 1997, Ranganathan *et al.* 2010).

Fig wasps may constitute a major source of food for ants. Indeed, Schatz *et al.* (2008) demonstrated on dioecious *Ficus* species that fig wasps on male trees provided a sufficiently abundant and reliable resource to allow continuous presence of dominant ants on the trees. However, whether fig wasps may constitute a sufficient resource in monoecious *Ficus* species is still an open question. Indeed, these species produce figs less frequently than dioecious ones and often present more synchronized crops (e.g. Shanahan *et al.* 2001). Hemipterans could constitute an alternative resource that could allow the continuous presence of tending ants on monoecious fig trees (Schatz *et al.* 2008). However, the presence of hemipterans and tending ants on monoecious fig species has been mainly reported from Africa and Madagascar (*F. sur* in South Africa [Compton & Robertson 1988, 1991; Zachariades 1994]; *F. vallis-choudae* in Cameroon [Dejean *et al.* 1997], and several fig species in Madagascar, Malawi, South Africa, Zambia, and Zimbabwe [Cushman *et al.* 1998]) while the most convincing data on fig wasps providing sufficient food for ants in dioecious figs stems from Borneo (Schatz *et al.* 2008). Hence, to confirm that continuous ant presence on monoecious fig trees is systematically

associated with the presence of hemipterans, we need to record whether in other parts of the world, ants on monoecious *Ficus* are systematically associated with hemipterans.

For ants, a fig tree may constitute an appropriate support presenting dispersed feeding sites, located exclusively in the arboreal stratum. Optimization of fig wasp capture efficiency could lead ants to inhabit this stratum in order to reduce distance between their nest and this food source in accordance with central place foraging theory (Stephens & Krebs 1986; Bell 1991; Schatz *et al.* 2008). Diverse reports of arboreal ant nests within fig trees support this hypothesis, and suggest that ants effectively find sufficient food sources within fig trees. Examples include nest location among the leaves of *F. fistulosa* for *Oecophylla smaragdina* and of *F. sur* for *O. longinoda* (Thomas 1988; Schatz *et al.* 2008), between grouped figs of the cauliflorous *F. botryoides* for unidentified Formicidae (Dalecky *et al.* 2003) and cauliflorous figs of *F. fistulosa* for *Crematogaster* sp. (Schatz *et al.* 2008), within figs of *F. sycomorus* by *Cardiocondyla wroughtoni* (Lupo & Galil 1985), in large persistent stipules (up to 80 x 20 mm) of *F. paracamptophylla* often tenanted by ants (Corner 1976), in ant gardens on *F. paraensis* and *F. trigona* for *Camponotus femoratus* and *Azteca* cf. *traili* (Davidson 1988; Benzing 1991) and within the dead parts of branches on *F. carica* by *Crematogaster scutellaris* (Schatz & Hossaert-McKey 2003). Moreover, one species of *Ficus* presents what appear to be structures specifically evolved to host ant nests (Maschwitz *et al.* 1996). This study showed that 64% of the opened structures they called domatia of *Ficus obscura* var. *borneensis* (included in *Ficus pisifera sensu* Berg & Corner 2005) were inhabited by ants, belonging to eight species distributed into five genera (*Camponotus, Cardiocondyla, Cataulacus, Crematogaster* and *Tetramorium*). Despite lack of description of ant behavior on this species, the presence of extrafloral nectaries and structures sheltering opportunistic ants on *F. obscura* var. *borneensis* suggests existence of a non-specific protection mutualism. Interestingly, in their field survey, Maschwitz et al. failed to detect similar structures in *Ficus* species belonging to over 20 other Malaysian fig species and they also failed to detect such structures in a survey of herbarium samples from 37 Australasian fig species.

In this study conducted in the island of Taiwan, we focused on the monoecious *Ficus subpisocarpa*. We describe here the presence of hollow structures

inhabited by ants in a fig tree associated with an plant-ant interaction. We determined the frequency of the hollow structures and the ant occupancy and we identified the observed ants to genus and describe traits of their presence. We also correlate ant presence and presence of hemipterans. We then discuss the insights into ant-fig interactions brought about by this discovery of a new case of ants inhabiting hollow structures in fig trees.

MATERIALS & METHODS

Ficus subpisocarpa Gagnep. is a monoecious fig tree belonging to subsection *Urostigma* (sensu Berg & Corner 2005). It is a hemiepyphitic or terrestrial tree which grows up to 7m in height distributed in South Asia from the South of Japan to Taiwan and to the Malay Peninsula and the Maluku Islands (Berg and Corner 2005). This species produces abundant crops, 2-4 times per year, of small cauliflorous figs, ripening over a 1-3 week period (Corlett 2006; Bain pers. obs. for Taiwan). As most species of subsection *Urostigma*, *F. subpisocarpa* is a deciduous tree presenting rhythmic growth (Berg & Corner 2005).

Hollowed stems hosting ants were incidentally noted on individual trees growing in Taiwan when inspecting trees for ant presence. To better describe and quantify this trait we examined branches from a series of individual trees. Branches were collected on eight trees: six in Taipei (National Taiwan University campus and Fuzhoushan Park), one 25 km north, at Bitou Cape on the North Coast of Taiwan and one 350 km south, in Kenting in the extreme south of the island. Five to 16 apical branches were sampled for each tree at their junction with a main trunk. Indeed such branches usually grow directly from the trunk or from main branches and usually wither without reaching more 60 cm (Bain pers. obs.).

For each branch we measured length, diameter of the branch at the cutting level, diameter at the middle of the apical internode and we counted the number of ramifications. Then the branches were split lengthwise, and the length of each hollow section (hereafter called cavity) was measured. Branch diameter was measured at the middle of the cavity as well as the distance from the branch apex.

When ants were observed in the cavity, the inner diameter of the cavity was measured and the number of exit holes noted. The cavities were characterized as described in Fig. 1 into six categories: young cavities empty or attacked

by insect larvae, inhabited and previously inhabited cavities, mature cavities, and old cavities. The sequence of the cavities from the apex was noted and for trees 02, 03, 04 and 06, the precise internodes, numbered from the apex, where the structures were observed were also noted. The insect content of inhabited cavities was collected, identified and counted. Ants were identified to genus using Bolton (1994) and Lin & Wu (2003).
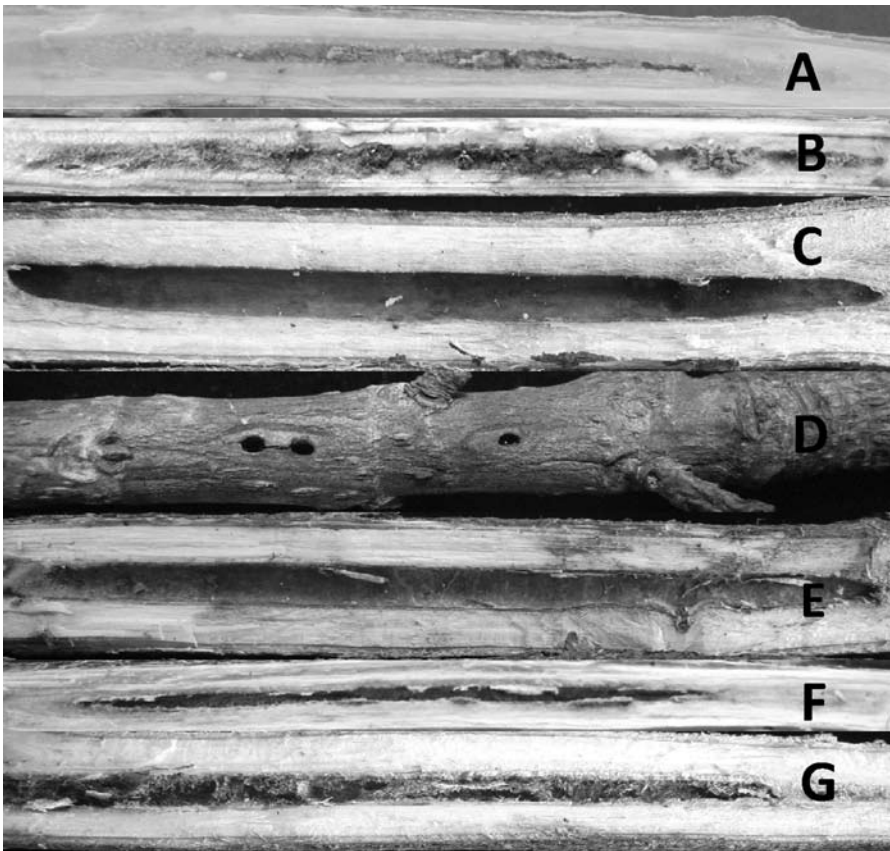

Fig. 1. The different types of cavities. A) Young cavity: these cavities are characterized by their young tissues. Only the central part is hollowed, the inner pith has not dried out yet. B) Young attacked cavity: the structure of the cavity is the same as for young cavities but insect larvae are feeding inside. C) Inhabited cavity: ants are observed inside. All pith tissue has been removed. D) Entry holes of an inhabited cavity. E) Formerly inhabited cavity: all the pith has been removed but no ant live inside. Often fungi or mould have grown on the inner surface. F) Mature cavity: the inner pith has dried out all along the internode. G) Old cavity: secondary growth is beginning to compress the cavity

An additional set of trees were examined for the presence of ants and of hemipterans to determine whether there was a frequent association. One hundred ten branches distributed on 11 trees located in Taipei were examined.

Additionally herbarium samples originating from Japan, Vietnam and Thailand were examined for the presence of similar hollow structures. They included samples of *Ficus subpisocarpa subpisocarpa, F. subpisocarpa pubipoda* C.C. Berg and the closely related *F. geniculata*. The herbarium samples examined were:

Ficus subpisocarpa Gagnep., JAPAN: Kagoshima Pref., Yaku Is., 20 May 1984, T. Yahara, T. Nagamasu & T. Kawahara 10340 (L); Ryukyu Islands, Misato-mura, Matsumo to-aza, 7 August 1951, E.H. Walker, S. Tawada, T. Amano 6441 (L); VIETNAM: Sai Wong Mo Shan (Sai Vong Mo Leng), Lomg Ngong Village, Dam-ha, Tonkin, July 18 – Sept 9, 1940, W.T. Tsang 30348 (L).

Ficus subpisocarpa Gagnep. subsp. *pubipoda* C.C. Berg. THAILAND: Ranong, Kaper, Laem Sohn National Park, sea level, 30 November 1996, J.F. Maxwell 96 – 1568 (L); Chiang Mai, Muang, Doi Sutep – Pui National Park, elevation 1350m, 26 March 2002, J.F. Maxwell 02 – 103 (L); Chaiyaphum, between Nam Phrom and Thungkamang, alt. 800m, 13 Dec 1971, C.F. van Beusekom, R. Geesink, C. Phengkhlai & B. Wongwan 4218 (L).

Ficus geniculata Kurz. VIETNAM: Cana province de Phanrang, 25 Oct 1925, M. Poilane 12491 (P); Ka Rom pr. Phanrang, 7 Mar 1924, M. Poilane 9964 (P); THAILAND: Lampang, Jae Home, Doi Jae Sawn National Park, alt. 425 m, 7 Jan 1992, J.F. Maxwell 92 – 16 (E); Tak, Mueang, Rd. No. 105, km 19 – 20, alt. 400 m, 21 Nov 2005, R. Pooma, C.C. Berg & M. Poopath 5734 (L).

RESULTS

Occurrence of cavities

Sampled branch length ranged from 21 cm to 156 cm. Ten percent of the studied branches presented no cavity, 36% presented a single cavity and 54% presented several cavities (Table 1). The average length and diameter (at cutting level) of branches did not differ between branches with and without cavity (Mann-Whitney U test, NS).

Table 1. Cavity data per tree. Cavity types are defined according to Fig. 1. The two undetermined cavities correspond to cavities that were damaged during sampling. All trees located in Taipei, except for Tree 7 located at Bitou Cape and Tree 8 located at Kenting.

				Tree					
	1	2	3	4	5	6	7	8	Proportion
Number of branches	13	10	10	16	12	10	10	5	
Young healthy cavity	11	6	4	3	4	3	3	1	0.172
Young attacked cavity	3	6	5	0	6	4	1	1	0.127
Inhabited cavity	3	4	0	0	16	7	1	1	0.152
Formerly inhabited cavity	0	0	0	1	9	1	1	0	0.059
Mature unused cavity	7	17	3	22	24	15	2	2	0.451
Old cavity	0	3	0	0	3	0	0	0	0.029
Undetermined	0	0	0	0	0	0	1	1	0.010
Total	24	36	12	26	61	30	9	6	

On the 86 analyzed branches, a total of 204 cavities were observed (2.4 ± 2.0 cavities per branch or 4.2 ± 3.1 cavities per meter). The number of cavities per branch varied significantly among trees from 0.90 to 5.0 (One-Way ANOVA $F_{6,79} = 11.85$; $p<0.001$) (Table 1).

The different types of cavities

We identified six kinds of cavities in *F. subpisocarpa* branches (Fig. 1): young cavities, intact or attacked by insect larvae, cavities inhabited by ants and cavities formerly inhabited by ants, mature cavities, old cavities. The most frequent hollow structures were mature cavities (45%), followed by young cavities (30%, 17% intact and 13% attacked by insect larvae) and inhabited cavities (15%). Young and mature cavities were observed on all trees. Cavities inhabited by ants were observed in six of the trees (75%), and a formerly inhabited cavity was observed on an additional tree. Two-third of the inhabited cavities sheltered ant pupae or larvae. Out of the 32 inhabited cavities, 7 were located on branches that presented a young cavity attacked by insect larvae (22% of the inhabited cavities): protection, if any, is not perfect.

Length of cavities

The length of most cavities (75) ranged from 2 to 14cm (Fig. 2). Four cavities measured less than 2cm and seven were longer than 22cm. Young cavities

were most frequent (46%) in the short length classes (L<4cm) and were overall significantly shorter than the other ones (One-Way ANOVA: $F_{1,233}$ = 12.72; p<0.001; average: 7.1±4.3cm). Mature cavities were most frequent in the seven following length classes (4cm<L<18cm). Only few cavities measured more than 18cm. Among these longer cavities, inhabited and formerly inhabited cavities represented 7 out of 16 cavities. Indeed inhabited cavities were overall significantly longer than other types of cavities (One-Way ANOVA: $F_{1,233}$ = 35.61; p<0.001; 14.1±7.0cm versus 8.8±5.5cm).

Location of the different cavity types on the branches

Fig. 3 A, B, C and D illustrates the pattern of branch growth in diameter and the distribution of cavity types according to distance from the apex. Diameter remained constant at about 7mm for the first 10cm from the branch apex, then from 10cm to 60cm from the apex the diameter progressively increased to about 12mm. Finally from 60cm to 130cm the branch diameter remained constant at about 12mm.
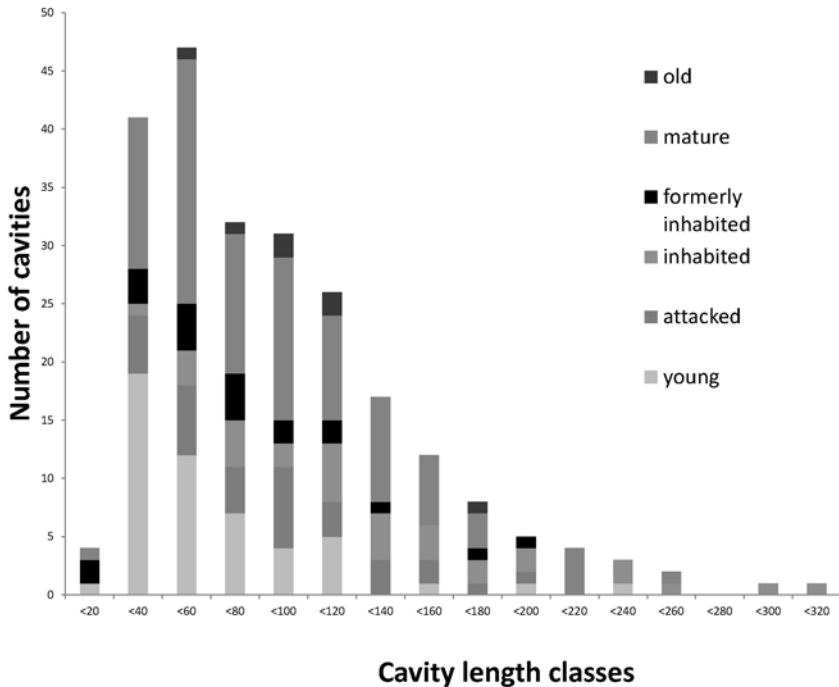
Fig. 2. Cavity length as a function of cavity type. Inhabited cavities are longer than average.

Young cavities (empty or attacked by insect larvae) seem to constitute a homogeneous class. They were mainly concentrated in the first portion up to 10 cm from the apex (respectively 55 and 56% of them), but also in the second portion up to 20 cm and they were present, though in lower numbers, up to 40 cm from the apex (respectively 94% of intact ones and 86% of attacked ones were located less 40 cm from the apex). They were significantly closer to the apex than other cavity types (One-Way ANOVA: $F_{1,221} = 32.37$; $p<0.001$). As a result, branch diameter at the level of young cavities was on average smaller than for other cavity types (One-Way ANOVA: $F_{1,237} = 48.91$; $p<0.001$),
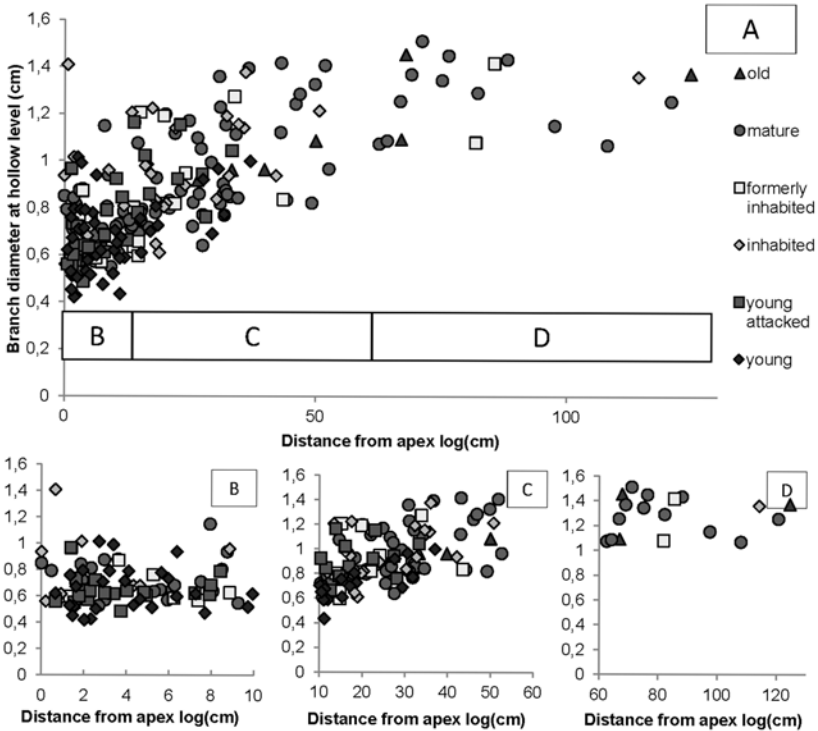

Fig. 3. A. Distance of the different types of cavities from the apex and branch diameter. B, C & D: Detailed views of portions of graph A. Note that young cavities are only observed up to 40 cm from the apex and inhabited cavities are mainly observed up to 50 cm from the apex.

Inhabited cavities and *formerly inhabited cavities* seem to form a second homogeneous class. They were present from the apical internode and concentrated in the first 35cm from the apex although some were observed further away from the apex.

Mature cavities seem to constitute a third class. They were observed at all distances from the apex.

Finally only few cavities were in the process of closing due to secondary growth and they were located from 26cm from the apex to 68cm from the apex. Statistically, mature and old cavities were grouped as the furthest from the apex (One-Way ANOVA: $F_{4,218} = 13.74$; $p<0.001$).

The young cavities (intact and attacked) were mainly the most apical cavity when the branches presented more than one cavity. Young cavities attacked by insect larvae were frequent at the most apical internode; they represented 33% of the cavities at this internode. On the other hand old cavities were observed only from the fourth to the eleventh internode from the branch apex. Mature cavities were the most common for all the ranks, and they were observed up to the eleventh internode. Inhabited cavities were only observed in the four apical internodes, with a peak frequency at the third internode (50% of the inhabited cavities were located on the third internode). When a single cavity was noted for a branch, the cavity was in 67% of the cases a young cavity (intact or attacked).

Ant species present within cavities

Four ant genera were observed within the cavities of *F. subpisocarpa* branches: *Crematogaster* (Myrmicinae), *Myrmica* (Myrmicinae), *Technomyrmex* (Dolichorinae) and *Prenolepis* (Formicinae). On the six trees presenting inhabited cavities, 32 inhabited cavities were observed on 21 branches. *Crematogaster* ants occupied 25 cavities (78% of the cavities), the three others genera occupied each two cavities. For the six branches presenting more than one occupied cavity (five branches with two occupied cavities and one with three), all were occupied by *Crematogaster*. One structure was shared by two species (*Crematogaster* sp. and *Prenolepis* sp.). This was in one of the few naturally open cavities, and ants from the two genera were living on each side of the open structure. The branches from trees 07 and 08 (Table 1) presented only one inhabited cavity each and the ants belonged both to

genus *Technomyrmex*. All other trees hosted a mix of *Crematogaster* ants and other genera.

Patterns of ant presence

When *Crematogaster* ants were present, workers were observed in all the inhabited structures and their number ranged from eight to 320 individuals. Larvae and pupae were present in 10 of the 25 occupied cavities (40%), winged *Crematogaster* adults in nine of them (36%) and queens in four (16%). In the *Prenolepis* inhabited cavities, the nest containing most workers (25 individuals) also contained larvae and pupae. The second one was the one shared with *Crematogaster* ants and sheltered only workers (16 individuals). One of the two cavities containing *Technomyrmex* contained 135 workers, nine queens, 51 pupae, 36 larvae but no winged adults, and the second one contained 37 workers, two queens, six pupae, three larvae and seven winged adults. Finally the two cavities inhabited by *Myrmica* ants presented fewer workers than for the other species (nine and 12 individuals), no winged males and both of them had two queens and winged females. In four cavities inhabited by *Crematogaster*, other ant species were also collected. In tree 05, all inhabited cavities contained *Crematogaster* ants but in two of them *Technomyrmex* ants were also collected inside the nest (one and six individuals). Moreover one *Prenolepis* ant was found in a cavity on tree 01, and this tree sheltered a sampled *Prenolepis* nest. Similarly, a *Myrmica* ant was found in a cavity inhabited by *Crematogaster* in tree 06, and that tree presented a cavity inhabited by *Myrmica* ants.

Crematogaster ants tended to inhabit longer and wider cavities than the other species (Fig. 4). Nevertheless, cavity diameter was independent of
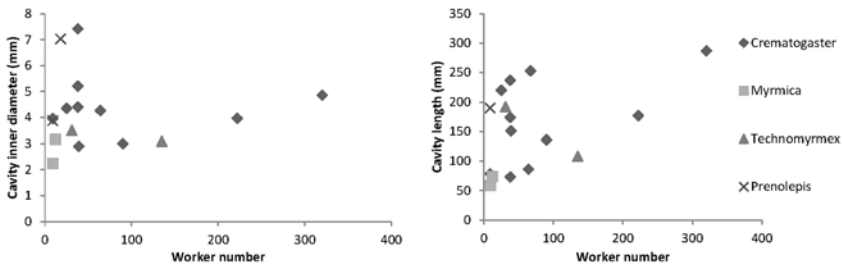

Fig. 4. Worker distribution according to cavity inner diameter (left) and to cavity length (right). Cavity diameter was measured at its mid point. Cavity diameter was independent of colony size.

branch diameter: all *Crematogaster* ants were living in similar-width nests. The ants of this genus were occupying cavities from very close to the apex to more than one meter away from the apex (Fig. 4).

Presence of other insects within cavities

Fig wasps (captured by ants) were found in six inhabited cavities. Both *Technomyrmex* nests contained fig wasps (the first one, one *F. subpisocarpa* female pollinating wasp (*Platyscapa ischiana*) and three wingless males and the second one, one *P. ischiana* female wasp and two female non-pollinating fig-wasps of genus *Sycoscapter*). Then one *Crematogaster* cavity contained two non-pollinating female wasps *Otitesella ako* (a genus whose precise oviposition period is species dependent, Compton 1993) while a second one contained a female non-pollinating fig wasp from genus *Sycoscapter* (a genus ovipositing after the pollinator in the fig development sequence; Tzeng et al. 2008). Finally in the cavity inhabited by two ant species two female *Platyscapa ischiana* were collected and 18 female *Sycoscapter sp.* The antennae and the ovipositors of the collected fig wasps had been cut off by the ants.

A scale insect (Hemiptera: Coccoidea) and an aphid (Hemiptera: Aphidoidea) were found in two distinct *Crematogaster* inhabited cavities. The larvae attacking young cavities were Coleopteran larvae. Finally, Curculionidae beetles (Coleoptera) were often observed on *F. subpisocarpa* branches (Bain, pers. obs.).

Correlation between presence of ants and presence of hemipterans

We frequently observed sap sucking insects on different vegetative parts of *F. subpisocarpa*. Scale insects were often observed on leaves and in shelters built by *Crematogaster* ants between figs or at the base of ramifications, but also occurred on figs, while aphids were almost only observed on figs. Ants were observed tending both scale insects and aphids. Ants, coccids and aphids were observed on the branches.

In the set of 110 branches that were specifically monitored for ant and hemipteran presences, ants were observed on 24 branches and were distributed into 3 genera: *Crematogaster* (23 branches), *Prenolepis* (1 branch, on which *Crematogaster* was also present) and *Myrmica* (1 branch). The branch presenting *Myrmica* ants presented no hemipterans, so in all cases when ants

were associated with hemipterans, *Crematogaster* ants were present on the branch.

We observed a correlation between the presence of *Crematogaster* ants and the presence of hemipterans on the 110 branches examined. Indeed, *Cremato-gaster* were observed on 23 branches and were associated with hemipterans in 20 cases, while hemipterans were present on 33 branches (correlation test on the cumulative observations: Kendall tau=0.940, p<0.001).

Aphids were mainly observed on figs (10 cases, often in association with coccids) as opposed to on the leaves (3 cases out of which two corresponded to winged individuals). In 8 out of 10 cases aphids were observed on figs, they were associated with *Crematogaster* ants. Coccids seemed to be much less specialised as the coccids were observed only in the cavities (2 branches), only on the leaves (12 branches), or both in the cavities and on the leaves (2 cases), on leaves and figs (4 cases) and in all three locations (4 cases).

Comparison with cavities observed in herbarium samples

Cavities similar to those observed in Taiwan were found in all herbarium samples from typical *Ficus subpisocarpa* Gagnep. collected in Japan and Vietnam, from *Ficus subpisocarpa* Gagnep. subsp. *pubipoda* C.C. Berg collected in Thailand and from *Ficus geniculata* Kurz collected in Vietnam and Thailand.

DISCUSSION

While the presence of a central cavity within the branches of fig trees is quite common, we demonstrated here that cavity traits in *F. subpisocarpa* allow a series of ant species to inhabit these cavities. After an analysis of occurrence of branch cavities in dioecious and monoecious fig species, we will examine how this trait may favor myrmecophytism, in conjunction with the different food sources exploited by ants on different *Ficus* species.

The presence of hollow internodes is well known though hardly investigated in *Ficus*. It is frequent in dioecious species as exemplified by the reference in the species name to fistulose branches in *Ficus fistulosa* Reinw. ex Blume, *Ficus fistulosa* Koord (= *F. congesta* Roxb.) and *Ficus fistulosa Kurz* (=*Ficus schwarzii Koord*). Corner (1967) stated that, in *F. cristobalensis*, twigs are 10-20 mm thick, with indistinct internodes and the wide pith is often hol-

lowed by ants. Nevertheless, quantitative reports on the presence of hollow internodes in live plant material and their use by ants in *Ficus* are basically lacking. We provide here a first report on the presence of hollow internodes in a monoecious fig species and on the colonization of these hollow internodes by ants. *Ficus subpisocarpa* presents hollow internodes all over its range, and hollow internodes are also present in its close relative *F. geniculata*. In *F. subpisocarpa* these hollow internodes are used by ants that make entry/exit holes to access the cavities. These occupied hollow internodes are located close to the branch apices.

While hollow internodes could be rather frequent in dioecious figs, they seem to be less frequent in monoecious figs of subgenus *Urostigma*. However, a characteristic trait of subsection *Urostigma* (about 23 species) to which *F. subpisocarpa* belongs, is intermittent growth, usually seasonal and accompanied with deciduousness (Berg & Corner 2005), as opposed to continuous growth in many subgenus *Urostigma* species. Fast growing plants often produce twigs presenting more pith than species producing slowly growing twigs. We suggest that quick growth of the twig associated with intermittent growth is a major feature at the origin of the hollow internodes in *F. subpisocarpa*.

Hollow internodes are a feature that may facilitate the evolution of myrmecophytism. Myrmecophytism also involves producing food (nectar, food bodies) that will stabilize the ant nests. *Ficus* provide ants with an access to fig-wasps, pollinators and parasites. While fig-pollinating wasps are present on the trees for short spells of time, at fig receptivity and at wasp emergence, parasites are present on the fig surfaces for longer periods of time. Schatz *et al.* (2008) suggested that cauliflory, the abundant production of figs on short specialized branches, allowed easier patrolling of figs by ants and thus could be conceived as a way of stabilizing ant nests in a tree and getting protection against parasitic wasps. While cauliflory is little represented in subgenus *Urostigma*, *F. subpisocarpa* as a number of species of subsection *Urostigma* is cauliflorous, producing numerous clusters of small figs on the branches. The species also fruits frequently producing 2-4 fig crops a year and a crop may ripen over a period of 3 weeks (Corlett 2006, Bain pers. obs.), two characters that increase the number and length of periods when fig-wasps can be used as a food source exploited by ants. This is all the more true as the ants, beyond pollinators, collected non-pollinating fig wasps ovipositing before

(*Otitesella*) and after (*Sycoscapter*) the pollinators, thus extending the period during which a crop provides food for ants. Intermittent growth, cauliflory, frequent fruiting and prolonged fig maturation period may constitute a set of characters of *F. subpisocarpa* that facilitate the establishment of a strong interaction with ants.

Nevertheless, despite these features, in monoecious figs, fig wasps may still not provide sufficient resources for ants to establish stable nests within fig branches. We hypothesize that beyond capturing fig wasps during their presence on figs (oviposition period and the period of emergence from figs), ants may also depend on hemipterans when fig wasps are less abundant. Several of our observations support this hypothesis. First, we observed hemipterans more frequently on branches colonized by ants, and we observed captured hemipterans (scale insects and aphids) within cavities inhabited by ants. Hemipterans present in *F. subpisocarpa* could thus constitute a regular source of both honeydew and prey. Ant-hemipterans interactions have previously been reported in two African monoecious fig species (Dejean *et al.* 1997; Zachariades *et al.* 2009), but we provide here the first observations of predation by ants in the fig context. More detailed studies will be required to investigate the contribution of hemipterans in the diet and maintenance of ants on fig trees. Second, fig wasps were found in six nests of *Crematogaster, Technomyrmex* and *Prenolepis* ants. On two dioecious fig species, ants (especially *Crematogaster* species) are also known to feed on fig wasps (Schatz *et al.* 2008), and to constitute strong non-pollinating wasp repellents (Schatz & Hossaert-McKey 2003). Non-pollinating fig wasps with cut ovipositors discovered in *F. subpisocarpa* cavities suggests that *Crematogaster* ants capture them while they are ovipositing with their ovipositor inserted through the fig wall, as observed on dioecious figs (Schatz *et al.* 2006, 2008). More detailed studies are required to determine the impact of ants on fig wasps population. Available data suggests that exploitation of both hemipterans and fig wasps as two permanent food sources may be sufficient to explain continuous ant presence in monoecious fig trees.

We also observed on the monoecious *F. subpisocarpa* that ants seem to predate more non-pollinating fig wasps than pollinating ones. This observation suggests a positive role of ants for the fig-fig wasp mutualism, acting here as indirect mutualists (Dawkins & Krebs 1979; Bronstein 1991; Schatz *et al.* 2006,

2008). Even if the impact of ants on the populations of hemipterans and fig wasps needs to be investigated in detail, we may surmise that the monoecious *F. subpisocarpa* may be selected to provide shelters for ant nests. Nevertheless, the caulinary cavities in which the ants nested are hardly sophisticated and the dwellers need to excavate the inner pith to be able to inhabit them and they have to create openings to gain access. Thus, the hollow structures of *F. subpisocarpa* branches sheltering ants should be considered as potential domatia precursors according to current terminology (Webber *et al.* 2007). In addition, the predominance of *Crematogaster* among ants inhabiting this fig species may appear as a trend towards specialization in this ant-plant interaction. Because we observed similar structures in the related *Ficus geniculata*, we may infer that the current level of association is quite old and that selective pressures are not strong enough to lead to the evolution of more specialized structures such as in the *Acacia* or *Macaranga* genera. Such results certainly incite further investigation about insects-fig interactions, and reinforce the status of fig trees as supporting complex networks of interactions (Compton and Robertson 1988; Zachariades 1994; Schatz & Hossaert-McKey 2003; Schatz *et al.* 2006, 2010).

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