A novel trophobiosis between ants (Hymenoptera: Formicidae) and a palm-feeding planthopper (Hemiptera: Cixiidae)

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Phloem-feeding Hemiptera (*i.e.* Sternorrhyncha, Fulgoromorpha and most Membracoidea) produce honeydew in amounts that often exceed the insect body mass several times per hour (Larsen *et al.* 1992). Although honeydew is a valuable food source for many insects, most Hemiptera just spray or kick it away. Trophobiotic interactions with Hymenoptera (ants, bees and wasps) is common only in Coccoidea, Aphididae and Membracidae, but rare in other hemipteran lineages (Delabie 2001). Within Fulgoromorpha, trophobiosis is known only from a few ground- and cave-living taxa (Delphacidae, Hypochthonellidae, Meenoplidae, Fulgoridae, nymphs of some Cixiidae: *e.g.* Hoch *et al.* 2006; Humphreys 1998; Naskrecki & Nishida 2007) and from many Tettigometridae, the latter with several adaptations to ant-attendance (Bourgoin 1997; Dejean *et al.* 2000).

Mutualism is most probable in situations where the cost of maintaining the situation is low to each participant, while the benefits are relatively great (Bristow 1991). In ant–hemipteran associations, ants benefit from reduced search time for food, honeydew or prey and benefit, in some cases to an extraordinary degree, *e.g.* Hill *et al.* (2003), from increased stability and quantity of the food resource. The advantages for Hemiptera include non-accumulation of honeydew on the substrate and protection from predators (Buckley 1987; Gullan & Kosztarab 1997; Hölldobler & Wilson 1990; Rozario *et al.* 1993).

In the course of field studies on the biology of endemic palm-feeding planthoppers in the Seychelles, we discovered the first example of an ant–hemipteran relationship involving an arboreal cixiid planthopper. The first evidence of the interaction is presented, and its origin and position within the range of different ant–hemipteran relationships is discussed.

Field studies in Seychelles were carried out in November and December 2006 and in September 2008. Planthoppers and ants were observed on the islands of Mahé and Silhouette on the endemic 'thief palm', *Phoenicophorium borsigianum* (Arecaceae), mainly in natural mid- and high-altitude forests. Interactions of *Fipsianus* with ants of the genus *Technomyrmex* were observed on Silhouette Island (Jardin Marron) and on Mahé Island (Mt Palmiste, Montagne Planeau, La Reserve, and several places within Morne Seychellois National Park), with ants of the genus *Anoplolepis* only at two sites, Mahé in Mare aux Cochons (7 November 2006) and Montagne Planeau (24 September 2008). Voucher specimens of ants and planthoppers were collected for identification and are stored in the Oekoteam collection in Graz, Austria.

Ants, mainly the native species *Technomyrmex albipes* (Smith, 1861), are the most abundant insects on leaves of the endemic palm, *Phoenicophorium borsigianum* (K. Koch.) Stuntz, present on 94 % of all leaves in high numbers (mean = 18.6, S.D. = ±13.3 ants per leaf). Among phytophagous animals, the endemic cixiid planthopper, *Fipsianus picturata* (Distant 1917), is the most abundant taxon (on 56 % of all leaves, mean = 2 hoppers; up to 15 hoppers recorded; Fig. 1). *Fipsianus picturata* is a medium-sized (4–5 mm), long-winged hopper species, feeding only on *P. borsigianum.* Adults sit on the upper side of the leaf, usually close to the midrib. Atypically for Cixiidae, adults (1) suck sap motionless in a given position for quite a long time unless disturbed and (2) often occur in larger numbers on one leaf (Fig. 2). Nymphs are most probably subterranean (Holzinger 2009)

Two types of interactions between ants and *F. picturata* were observed: very frequently, foraging *Technomyrmex* workers, in one case also *Camponotus thomasseti* Forel, 1912, touched hoppers with their antennae. Although ants are potential predators, *F. picturata* individuals showed no escape attempts, neither jumping nor flying, but stayed still. After a moment, the ant passed by and continued foraging.

The second interaction involved a much higher degree of mutualism. It was observed only with the 'crazy ant', *Anoplolepis gracilipes* (F. Smith, 1857). An *A. gracilipes* worker, sometimes two or

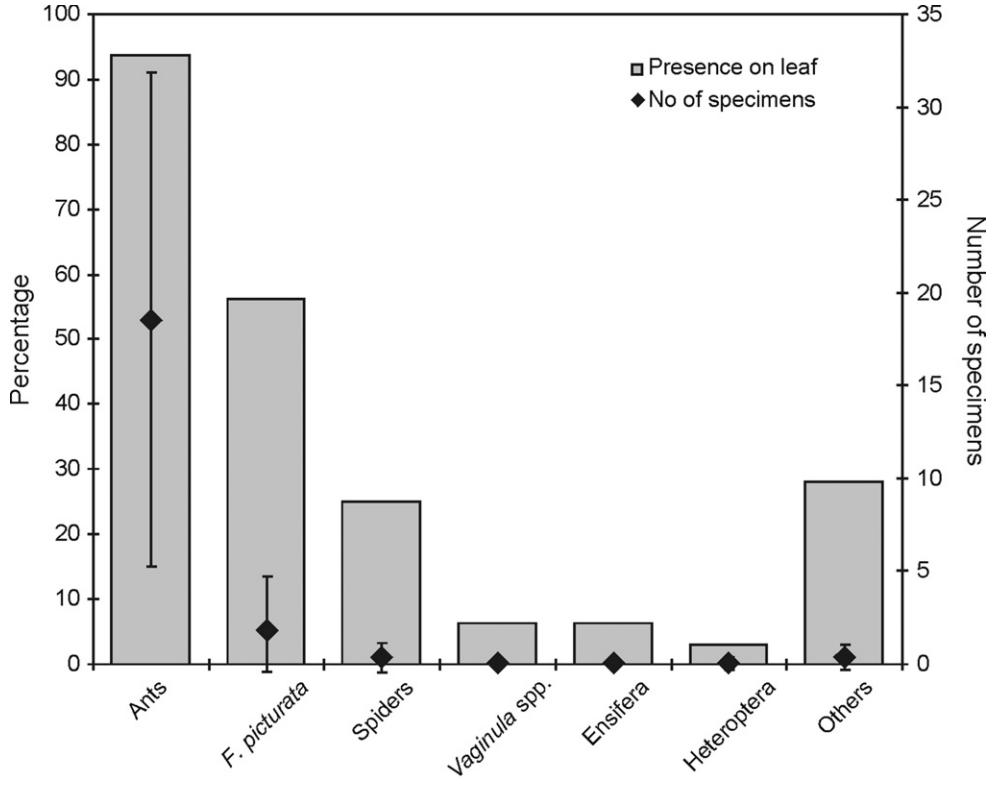

Fig. 1. Presence (columns) and abundance (diamonds) of animal taxa (males and females) on *Phoenicophorium borsigianum* leaves (upper side only; Seychelles, Silhouette, Jardin Marron, 20 September 2008, $n = 32$). 'Ants' refers mainly to *Technomyrmex*, *Vaginula* is a slug (Gastropoda: Vaginulidae), 'Others' includes various other Hemiptera, other arthropods and geckos (*Phelsuma* sp.).

three, Fig. 3, positioned itself behind the hopper and from time to time moved the tips of its antennae along the forewings of the hopper. Occasionally the hopper prepared to secrete a droplet of honeydew by raising its abdomen, then excreted a droplet that the worker immediately took with its mouthparts and drank (Fig. 4).

According to Bourgoin (1997: 121), all previously-known, durable ant–planthopper interactions occur only 'when planthoppers are either unable to escape (underground in ant galleries or under shelter) or sessile species (Tettigometridae)' and 'when planthoppers are either forced into gregariousness (cixiids kept in ant nests, delphacids kept under ant shelters) or when they are subsocial (tettigometrids)'. Thus, this is the first evidence of ant-attendance in an arborial planthopper that is saltatory, and the first evidence of such a relationship in adult cixiids.

Bourgoin (1997) distinguishes four main types of ant-attendance in Fulgoromorpha:

Fig. 2. Five specimens of *Fipsianus picturata* sitting along the midrib of a *Phoenicophorium borsigianum* leaf.

Fig. 3. Three workers of *Anoplolepis gracilipes* awaiting honeydew from a *Fipsianus picturata* female.

1. Opportunistic or occasional attendance: planthoppers deposit honeydew drops randomly; the honeydew is collected from the substrate by ants.
2. Underground attendance in ant nests.
3. Attendance of planthoppers under shelters built by ants.
4. Ants collecting honeydew drops directly at the anal opening and regularly antennating the planthoppers.

The interaction between *Fipsianus* and *Technomyrmex* most probably represents the first, 'simplest' type of interaction. Although no honeydew collecting by ants was observed, the absence of any escape attempts of *Fipsianus* indicates a kind of mutualism, or tolerance, at least between the two species. The interaction between *Fipsianus* and *Anoplolepis* meets the fourth, much more sophisticated type of trophobiosis. Our observations indicate that ant–*Fipsianus* relationships are facultative for *Fipsianus*. The loose *Fipsianus*–*Technomyrmex* relationship is most probably very old (perhaps even millions of years), as both species are endemics of the granitic Seychelles islands. In contrast, the intense *Fipsianus*–*Anoplolepis* trophobiosis is apparently very new, as *A. gracilipes* is an introduced species first reported from Seychelles in 1969 (Hill *et al.* 2003). It is quite

Fig. 4. An *Anoplolepis gracilipes* worker drinking a honeydew droplet secreted by a *Fipsianus picturata* female.

amazing that *F. picturata* displays a fairly loose mutualism with the endemic *T. albipes* while its trophobiotic relationship with the introduced ant species (less than 40 years ago) appears to be far more close. This supports the assumption that while ant–fulgoromorphan relationships seem to be a pleisomorphic behavioural trait, given the distribution among Fulgoromorpha taxa (see Bourgoin 1997), the degree of mutualism is not dependent on phylogenetic age.

Unlike most adult Cixiidae, *F. picturata* is predisposed towards ant attendance, due to its subgregarious and sedentary behaviour (*cf.* Way 1963). It therefore appears that the alien ant species *A. gracilipes* opportunistically utilizes an otherwise underutilized food resource, the honeydew.

Trophobiotic interactions between ants and Hemiptera have potentially broad ecological effects, as they dramatically alter the abundance and predatory behaviour of ants on plants (Styrsky & Eubanks 2007; Grover *et al.* 2008). The 'crazy ant' *A. gracilipes* is among the alien species with highest impact on natural ecosystems (*e.g.* Haines & Haines 1978a,b; Haines *et al.* 1994; Green *et al.* 1999; O'Dowd *et al.* 2003, Global Invasive Species Database 2008). It has a broad diet, but the availability of honeydew resources might limit population growth (Holway *et al.* 2002). The results presented here emphasize the extraordinary ability of *A. gracilipes* to utilize new honeydew sources, which might be one of the major causes for its colonization success. The newly discovered differential trophobiotic relationship between *F. picturata,* endemic to the Seychelles, and native and non-native ant species offers a prime opportu-

nity to study not only the evolution of ant–planthopper mutualism, but also how invasive species build new niches by utilizing previously non-utilized food resources, in a narrow time-frame.

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