

# Impact of an invasive alien ant, *Wasmannia auropunctata* Roger., on a specialised plant–ant mutualism, *Barteria fistulosa* Mast. and *Tetraponera aethiops* F. Smith., in a Gabon forest

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**Abstract.** 1. In tropical West Africa, the ant *Tetraponera aethiops* obligately inhabits the domatia of *Barteria fistulosa* trees, aggressively defending the trees from herbivory and pruning off lianas.

2. We compared the occurrence of ants and lianas on *B. fistulosa* trees in areas of Gabon, where the invasive little fire ant, *Wasmannia auropunctata*, was absent (uninfested area) and present (infested area).

3. We found that *T. aethiops* occurred significantly more often in larger *B. fistulosa* trees, and that occurrence rates were much higher in the uninfested area versus the infested area: on < 1 m trees: 17% vs. 0%; 1–5 m trees: 58% vs. 3%; > 5 m trees: 90% vs. 10%.

4. In contrast, lianas occurred significantly less often in the uninfested area versus the infested area: on < 1 m trees: 0% vs. 100%; 1–5 m trees: 0% vs. 77%; > 5 m trees: 10% vs. 63%.

5. In the infested area, *W. auropunctata* occurred significantly less often in larger *B. fistulosa* trees (on < 1 m trees: 100%; 1–5 m trees: 97%; > 5 m trees: 90%). Here *T. aethiops* and *W. auropunctata* coexisted on few trees (on < 1 m trees: 0%; 1–5 m trees: 1%; > 5 m trees: 4%).

6. The negative consequences for the trees are already evident, and the situation for native ants is likely to decline further in future because they will not be able to generate the large (relatively resistant) colonies found on large trees.

**Key words.** *Barteria fistulosa*, Gabon, interspecific competition, invasive ant, *Tetraponera aethiops*, *Wasmannia auropunctata*.

## Introduction

Ant–plant interactions are very diverse and are characterized by a variety of relationships, from simple voluntary and non-specific associations (opportunistic mutualism) (McKey

*et al.*, 1999) to obligate and specific associations (symbiotic mutualism) (McKey *et al.*, 1999).

African tropical forests are home to many cases of opportunistic mutualisms, and to obligate mutualisms such as the ant *Petalomyrmex phylax* and the plant *Leonardoxa africana* (McKey *et al.*, 1999; Brouat *et al.*, 2001). The ant continually rids its host plant of lianas or plants that can compete with it (Bequaert, 1922; Janzen, 1972; Yumoto & Maruhashi, 1999), also protecting against insect and

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mammalian herbivores (Janzen, 1972; McKey, 1974; Dejean *et al.*, 2008b).

*Barteria fistulosa* is characterized by an obligate association with the very aggressive ant species *Tetraponera aethiops* (Breteler, 1999; Djiéto-Lordon & Dejean, 1999). *Tetraponera aethiops* lives exclusively on its host plant, establishing nests in domatia on branches and eating extra-floral nectar (Dejean *et al.*, 2008a) as well as honeydew, released by Homoptera that also inhabit the tree's domatia (Yumoto & Maruhashi, 1999). All domatia are colonised first by the queens of *T. aethiops*. The queens stay inside the domatia for at least 6 months before production of the first workers, which open the domatia and begin to protect the tree against insect herbivores and competing lianas (Janzen, 1972; Yumoto & Maruhashi, 1999).

*Wasmannia auropunctata*, the little fire ant, is native to the Neotropical region (Kempf, 1972; Wetterer & Porter, 2003). Although this ant is firstly a litter inhabitant in its native range, it can nest opportunistically in cavities on tree trunks (Clark *et al.*, 1982) or in association with Hemiptera (Delabie, 1988). Its introduction to Gabon prior to 1913 is the earliest known appearance of *W. auropunctata* outside the Neotropics (Santschi, 1914). The Gabonese populations are genetically similar to those found in Guadeloupe, New Caledonia, and Tahiti (Foucaud *et al.*, 2010). Wherever they are found outside their native range, they have a negative impact on native biodiversity.

*Wasmannia auropunctata* is one of 17 ant species listed in the IUCN invasive species database. Invasive species in general are frequently stated to be the second greatest global threat to biodiversity, after habitat reduction (GISP, 2008). *Wasmannia auropunctata* bites the skin of humans and domestic mammals such as cats (Wetterer *et al.*, 1999), and may affect wild animals such as elephants, bush pigs, panthers, and leopards (Wetterer *et al.*, 1999; Walsh *et al.*, 2004). Its impact on the diversity of local, epigeic ants has been documented in Gabon (Walker, 2006; Mikissa *et al.*, 2008), the Galapagos Islands (Clark *et al.*, 1982), New Caledonia (Jourdan, 1997; Le Breton *et al.*, 2003), and more recently Israel (Vonshak *et al.*, 2010). However, the impact of *W. auropunctata* invasions on arboreal ants is less well documented, and even less is known about ants in strict association with host plants.

Here we investigate two questions about the impact of *W. auropunctata* on *T. aethiops*. (i) Does *W. auropunctata* competitively exclude *T. aethiops*? (ii) Does *W. auropunctata* disrupt the mutualism between *T. aethiops* and *B. fistulosa*?

We hypothesize that (i) the proportion of *T. aethiops* is lower in *W. auropunctata*-infested areas than in noninfested areas; and (ii) the proportion of *B. fistulosa* trees inhabited by *T. aethiops* is lower in *W. auropunctata*-infested areas than in noninfested areas.

## Methods

### Study sites

The study was conducted in two locations separated by several hundred kilometres. Both areas were formerly disturbed

and have since regenerated, with *B. fistulosa* being abundant along the forest edges.

The first site in Ekouk, Gabon (0°09'S, 10°32'E) was a patch of secondary forest in a former logging zone, replanted with rubber trees and bamboos and then abandoned, with an area of *Aucoumea klaineana* Pierre. reforestation. According to the local population, the presence of *W. auropunctata* was first reported in the area in 1970, and in the rubber plantations in 1990. An area where *W. auropunctata* is absent (uninfested area), characterized by the presence of *A. klaineana* reforestation, was selected as a control site.

The second site was within Lopé National Park (0°20'S, 11°60'E), in an area of secondary forest (logged until 1975) called 'the airport forest', which is characterized by a high density of *W. auropunctata*, present since at least 1965 (Wetterer *et al.*, 1999). The western part of this forest is not infested with *W. auropunctata* and was selected as a control site. All work was conducted in May 2006 and between March 2007 and August 2007.

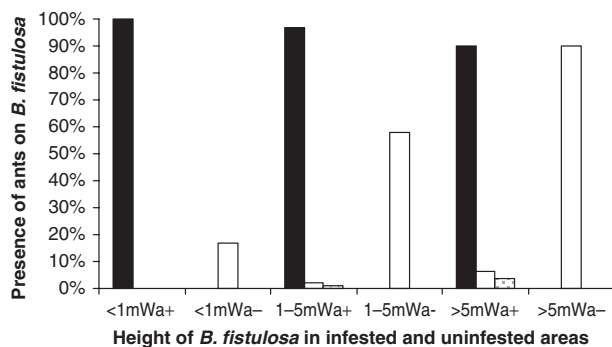
### Occupation of *B. fistulosa* trunks by ants and lianas in Lopé

To assess the relative occupation of the two ant species on *B. fistulosa*, we sampled 307 *B. fistulosa* trees in an area infested with *W. auropunctata*, ranked on a scale of size (19 trees were < 1 m high, 101 were between 1 and 5 m, and 187 were > 5 m). In an uninfested area, 233 *B. fistulosa* trees were sampled (12 trees were < 1 m high, 152 were between 1 and 5 m, and 69 were > 5 m).

Each *B. fistulosa* was measured and the presence of ants was recorded by direct examination of the tree. In areas of infestation, *W. auropunctata* were easily visible on the trees because workers are highly abundant and form large trails. However, in order to detect *T. aethiops* it was necessary to tap the trees gently to agitate workers into emerging from their domatia. The growth potential of *B. fistulosa* was also assessed by noting the presence or absence on the trunk and branches of lianas, which reduce tree growth (Federle *et al.*, 2002). However, those lianas were not identified to species. Statistical analysis on the presence of the two species of ants on *B. fistulosa* was carried out using Fisher's exact test, and on the presence of lianas by a Yates-corrected  $\chi^2$  test using STATISTICA® 6.0.

### Occupation of *B. fistulosa* domatia by ants at Ekouk and Lopé

To test the ability of *W. auropunctata* to occupy domatia inhabited initially by *T. aethiops*, because *W. auropunctata* is unable to open domatia unexcavated, we sampled 38 *B. fistulosa* (13 at Ekouk and 25 at Lopé) at heights between 2 and 4 m in both infested and uninfested areas. All branches were opened longitudinally from the base to the apex with secateurs, to enable the sampling of domatia. A total of 610 domatia were sampled: 229 in infested areas (111 at Ekouk and 118 at Lopé), and 381 in uninfested areas (73 at Ekouk and 308 at Lopé). We divided domatia into two types: those with ants (either species), or without ants (unexcavated).



**Fig. 1.** Presence of *Wasmannia auropunctata* and *Tetraoponera aethiops* on *Barteria fistulosa* trees < 1 m, 1–5 m, and > 5 m high at Lopé. (◻) *T. aethiops*; (■) *W. auropunctata*; (◻) coexistence of ants; (Wa+) infested areas; (Wa-) uninfested areas.

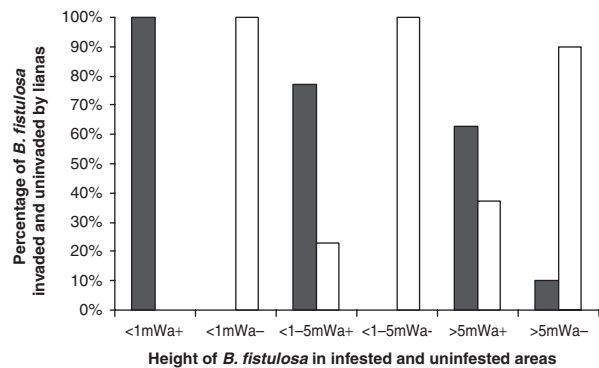
Domatia occupation was analysed using permutation tests (STATXACT® 7.0) to compare means of two independent groups (in each locality, Lopé or Ekouk).

## Results

### Occupation of *B. fistulosa* trunks by ants and lianas in Lopé

Our results show that firstly, for trees < 1 m high in uninfested areas, *T. aethiops* was present in a minority of trees (17%), and in infested areas *T. aethiops* was totally absent and all plants were patrolled by *W. auropunctata* workers. Secondly, for trees between 1 and 5 m high, the proportion of *T. aethiops*-inhabited trees was significantly lower in infested than in noninfested areas (2% and 58%, respectively, Fisher's exact test,  $P < 0.0001$ ), whereas the proportion of *W. auropunctata*-inhabited trees was significantly higher in infested than in noninfested areas (97% and 0%, respectively, Fisher's exact test,  $P < 0.0001$ ). In infested areas, *T. aethiops* coexisted with *W. auropunctata* in 1% of trees. Thirdly, for trees > 5 m, the proportion of trees inhabited by *T. aethiops* was significantly lower in infested than in noninfested areas (6% and 90%, respectively, Fisher's exact test,  $P < 0.0001$ ), whereas the proportion of *W. auropunctata*-inhabited trees was significantly higher in infested than in noninfested areas (90% and 0%, respectively, Fisher's exact test,  $P < 0.0001$ ). In infested areas, *T. aethiops* coexisted with *W. auropunctata* in 4% of trees (Fig. 1).

Our results also show that the invasion of the host tree by *W. auropunctata* is associated with the presence of lianas (Fig. 2). The percentage of trees overgrown with lianas was significantly higher in infested than in uninfested areas ( $\chi^2$  test corrected by Yates,  $P < 0.0001$ ). For example, for trees < 1 m high in uninfested areas, no trees were invaded by lianas; whereas in infested areas, all trees (100%) were invaded with lianas. Secondly, for trees between 1 and 5 m high in uninfested areas, no tree was invaded with lianas; whereas 77% of sampled trees in infested areas were overgrown with lianas. Thirdly, for trees > 5 m, in uninfested areas 10% of



**Fig. 2.** Encroachment of *Barteria fistulosa* according to their size at Lopé. (■) *B. fistulosa* invaded by lianas; (◻) *B. fistulosa* not invaded by lianas; (Wa+) infested areas; (Wa-) uninfested areas.

the trees were overgrown with lianas, compared with 63% in infested areas.

### Occupation of *B. fistulosa* domatia by ants

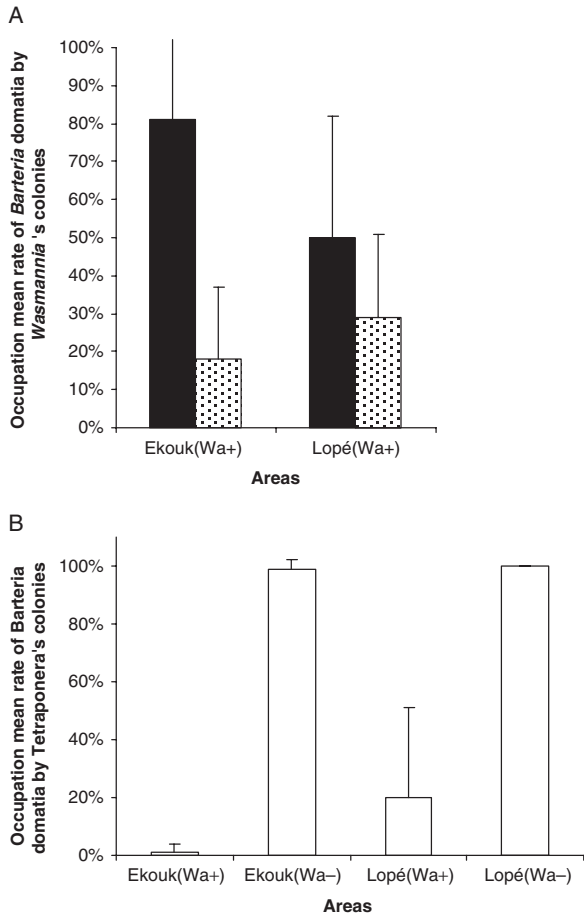
Our results show firstly that at Ekouk, in the infested areas, 81% of domatia were occupied by *W. auropunctata* and 18% of unexcavated domatia then remained unoccupied (Fig. 3a). However, the proportion of domatia occupied by *T. aethiops* was significantly lower in infested compared with noninfested areas: fewer than 1% of domatia were occupied by *T. aethiops* in the infested areas compared with 99% of domatia in the noninfested areas (permutation test,  $P < 0.001$ ; Fig. 3b).

Secondly, at Lopé, within the infested areas, *W. auropunctata* occupied 50% of domatia and 29% remained unexcavated (Fig. 3a). The proportion of domatia occupied by *T. aethiops* was significantly lower in infested compared with noninfested areas: fewer than 20% of domatia were occupied by *T. aethiops* in the infested areas compared with 100% of domatia in the non-infested areas (permutation test,  $P < 0.0001$ ; Fig. 3b).

Thirdly, *W. auropunctata* is able to establish populations inside the domatia in relation to the average numbers of queens, eggs, and workers. Thus in Ekouk areas there were average numbers of 0.06 queen, 14.15 eggs, and 77.24 workers per domatia; in Lopé areas no queens were found in domatia, but there were average numbers of 3.81 eggs and 47.24 workers per domatia (Fig. 4).

## Discussion

Our results showed that *T. aethiops* occupied a low percentage of *Barteria* trees in infested areas. It is well documented that outside its native range, *W. auropunctata* can exclude 90% of litter ant fauna (Clark *et al.*, 1982; Jourdan, 1997; Le Breton *et al.*, 2003; Wetterer & Porter, 2003; Walker, 2006). Furthermore, *W. auropunctata* can nest on trees (Clark *et al.*, 1982). This suggests that *W. auropunctata* has a superior competitive ability and kills *T. aethiops* colonies associated



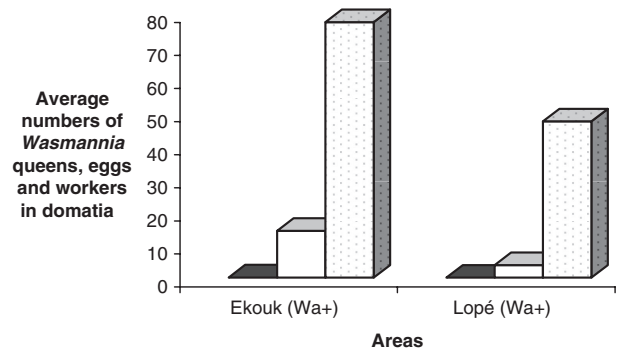
**Fig. 3.** Occupancy mean rate of *Barteria* domatia by *Wasmannia auropunctata* colonies in infested areas (Wa+) in Ekouk and Lopé (a); and by *Tetraponera aethiops* colonies in infested areas (Wa+) and uninfested areas (Wa-) in Ekouk and Lopé (b). (■) *W. auropunctata*; (□) *T. aethiops*; and (▣) unexcavated domatia.

with its polygyny and its opportunistic behaviour in nest occupation.

Interestingly, *T. aethiops* was able to persist in both medium-height and tall trees. We hypothesize that both medium and tall *B. fistulosa* trees house the largest *T. aethiops* colonies, which are better able to resist invasion.

In this study, the ground-level density of *W. auropunctata* was so high that the seedlings of *B. fistulosa* were completely invaded, and this phenomenon seemed to prevent any colonization of *T. aethiops* on these trees. The replacement of *W. auropunctata* on *B. fistulosa* is correlated with invasion by lianas, as shown by the number of seedlings competing with lianas. This effect is also exerted on the larger trees in the infested compared with the uninfested areas, where *T. aethiops* frequently destroys the lianas around trees (Janzen, 1972; Yumoto & Maruhashi, 1999).

Also, if domatia remained unexcavated within the infested areas, the explanation may be that (i) *W. auropunctata* queens are unable to open domatia of seedlings because they have been previously colonised by *T. aethiops* queens; (ii) the presence



**Fig. 4.** Population of *Wasmannia auropunctata* in domatia in Ekouk and Lopé areas: (■) queens; (□) eggs; (▣) workers.

of *W. auropunctata* on *B. fistulosa* trunks stops *T. aethiops* from colonizing those unexcavated domatia. It is well known that *T. aethiops* lives exclusively in domatia of its host plant (Janzen, 1972; Yumoto & Maruhashi, 1999).

A recent study by Dejean *et al.* (2008a) on the succession of ant species in relation to growth in three tree species (*Lophira alata* Banks ex Gaertn., *Anthocleista vogelii* Planch., and *B. fistulosa*) showed that *T. aethiops* drove *Crematogaster striatula* Emery., *Tetramorium aculeatum* Mayr., and *Oecophylla longinoda* Latreille. from its host tree. The only species able to resist was *Crematogaster impressa* Emery., which is able to occupy a few domatia released by *T. aethiops* without direct interaction. In that study, *W. auropunctata* occupied domatia through permanent exclusion of the arboreal ant. Thus *W. auropunctata* behaves like a parasite of the *B. fistulosa*–*T. aethiops* mutualism as per Yu (2001), or *W. auropunctata* usurps *T. aethiops* from its ecological niche. This is not surprising as prior studies have documented that invasive ants disrupt mutualistic seed dispersal interactions with many plants and other insects (Bond & Slingsby, 1984; Holway *et al.*, 2002; Lach, 2003). Another case of mutual exclusion has been documented between *Petalomyrmex phylax* Snelling. and *Cataulacus mckeyi* Snelling. on the tree *Leonardoxa africana* Baill. Aubrev. (Gaume & McKey, 1999).

Moreover, the sting used by *T. aethiops* against herbivorous insects (Lepidoptera, Coleoptera, and Orthoptera; Dejean *et al.*, 2008b) is paradoxically not used at all against *W. auropunctata*, probably because of the difference in size between the two species (McGlynn, 1999, 2000).

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