

Immediate impacts of invasion by *Wasmannia auropunctata* (Hymenoptera: Formicidae) on native litter ant fauna in a New Caledonian rainforest

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Abstract For the last 30 years, *Wasmannia auropunctata* (the little fire ant) has spread throughout the Pacific and represents a severe threat to fragile island habitats. This invader has often been described as a disturbance specialist. Here we present data on its spread in a dense native rainforest in New Caledonia. We monitored by pitfall trapping the litter ant fauna along an invasive gradient from the edge to the inner forest in July 1999 and March 2000. When *W. auropunctata* was present, the abundance and richness of native ants drops dramatically. In invaded plots, *W. auropunctata* represented more than 92% of all trapped ant fauna. Among the 23 native species described, only four cryptic species survived. *Wasmannia auropunctata* appears to be a highly competitive ant that dominates the litter by eliminating native ants. Mechanisms involved in this invasive success may include predation as well as competitive interactions (exploitation and interference). The invasive success of *W. auropunctata* is similar to that of other tramp ants and reinforces the idea of common evolutionary traits leading to higher competitiveness in a new environment.

Key words: ant diversity, biological invasion, New Caledonia, *Wasmannia auropunctata*.

INTRODUCTION

In the Pacific area, New Caledonia is recognized as a unique biodiversity hot spot (Myers *et al.* 2000). In this highly endemic context, the spread of exotic organisms through human agency is a major concern. One spectacular invasion is the rapid spread of the little fire ant, *Wasmannia auropunctata* (Jourdan 1997a, 1999). Native to the New World, the present distribution of this tiny stinging ant is nearly pantropical (Jourdan *et al.* 2002). *Wasmannia auropunctata*, which belongs to the 'tramp ant' group, exhibits biological characteristics (polygyny, the budding of new nests, unicoloniality, opportunism for food and nest location, fast nest relocation after perturbation) that facilitate its spread through human-mediated dispersal (Hölldobler & Wilson 1990; Passera 1994; McGlynn 1999). As a result, it is recognized as one of the worst exotic pest ants (Lowe *et al.* 2000), along with *Anoplolepis gracilipes* (the yellow crazy ant), *Linepithema humile* (the Argentine ant), *Pheidole megacephala* (the big-headed ant) and *Solenopsis invicta* (the red imported fire ant). In the Pacific area, it is an important threat that has been intercepted regularly by quarantine services since at least the mid 1960s (Wilson & Taylor 1967).

This small myrmicine, recorded for the first time in New Caledonia in 1972 (Fabres & Brown 1978), has now invaded a wide array of habitats on the main island, the Loyalty Islands, the Isle of Pines and even the remote inhabited island of Walpole (Jourdan 1997a). Several surveys in New Caledonia have confirmed the disruption of natural communities, especially in sclerophyllous habitats (Jourdan 1997a; Jourdan *et al.* 2001). This situation is in strong contrast to what one can observe in its natural range where it does not appear as a dominant species (Tennant 1994). Nevertheless, when disturbance occurs, outbreaks may be observed, so that Majer and Delabie (1999) considered this ant species to be a disturbance specialist.

Here we focus on the spread of *W. auropunctata* in a patch of rainforest on ultramafic soils and its apparent effect on the original ant community along the invasive gradient.

METHODS

Study area

This study was conducted in the Rivière Bleue provincial park, located in southern New Caledonia on ultramafic soils. Based on information gathered during botanical surveys, this forest is considered as pristine and undisturbed rainforest (Jaffré & Veillon 1990). The

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flora is highly endemic (89%) and dominated by Myrtaceae and Rubiaceae. *Wasmannia auropunctata* was first detected in the park in mid-1997 where its introduction and spread seemed related to the development of recreational areas (camping sites) through the use of contaminated construction material or caterpillar vehicles. In July 1999, we investigated a forest patch where the edge had been invaded by *W. auropunctata*. We conducted a trapping program to assess the extent of the invasion and to evaluate its impact on the native ant species community. We repeated this survey in March 2000 to assess the spread of the *W. auropunctata* population after 8 months.

Sampling of the ant community structure

Ant species richness and abundance were monitored by pitfall trapping along parallel transects, extending from the forest edge to 130 m inside the forest, deliberately placed across the invasion front. The pitfall traps consisted of plastic containers (58 mm internal diameter). They were half filled with a mixture of diethylene glycol and 2% formaldehyde as a preservative (Bestelmeyer *et al.* 2000). For each sampling period, 168 pitfall traps were arranged in six parallel lines of 28 traps each, with 5 m between the traps and 5 m between the transects. Traps were left open for 7 days. Although pitfall traps are more effective for trapping epigaeic ants in open habitats than in rainforest (Andersen 1991), this method provides a reasonably good estimation of species composition and relative abundance of ground surface-active ants (Bestelmeyer *et al.* 2000; Wang *et al.* 2001).

The ants were sorted to species level and species abundance was noted for each trap. Given the poor state of taxonomic knowledge of New Caledonian ants, species that could not be named were designated as a morphospecies with letter codes. All collected ants were deposited in the Institut de Recherche pour le Développement collection in Nouméa.

Statistical analyses

The pitfall data were pooled into seven groups that correspond to seven zones from the edge to the inner forest: 0–20 m; 20–40 m; 40–60 m; 60–80 m; 80–100 m; 100–120 m; and 120–135 m.

First, for each sampling period, we compared (for *W. auropunctata* and native species separately) the abundance in each zone by applying a Kruskal–Wallis one-way analysis of variance on ranks. Post-hoc multiple comparison tests (Dunn's tests) were subsequently used separately for *W. auropunctata* and native species, to isolate the zone or zones that differ from the others. Finally, we compared the abundance

of *W. auropunctata* and native species gathered in each zone between the two sampling periods by applying a Wilcoxon signed rank test. All statistical tests were carried out using SigmaStat software version 2.03 for Windows.

RESULTS

Distribution of *Wasmannia auropunctata*

Wasmannia auropunctata workers were detected foraging in the forest up to 85 m in July 1999 and 90 m in March 2000 from the forest edge. The abundance of *W. auropunctata* was highest in the zones near the forest

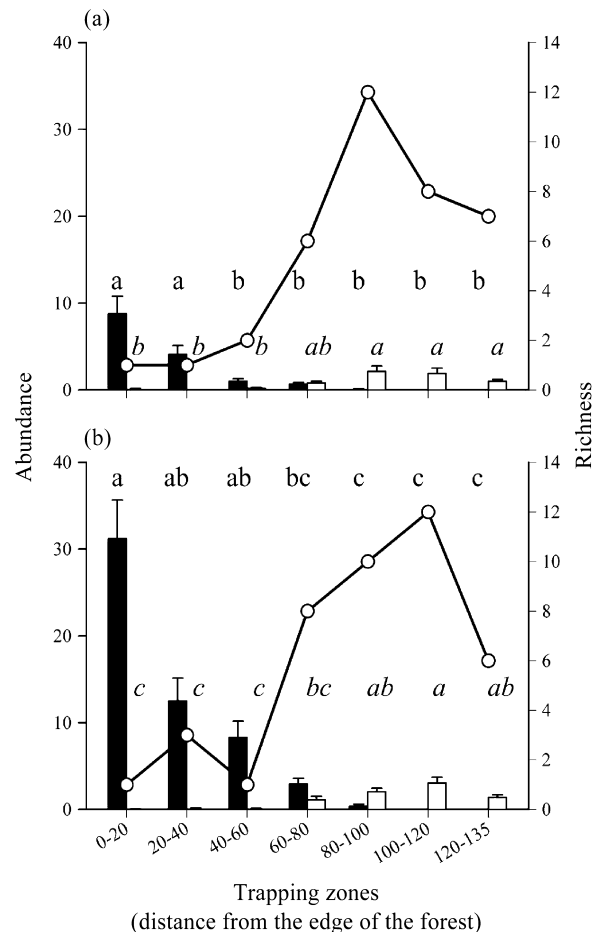


Fig. 1. Results of pitfall trapping along an invasive gradient in a New Caledonian rain forest in (a) July 1999 and (b) March 2000. Bars consist of mean \pm SE. For statistical comparisons we conducted a Kruskal–Wallis ANOVA followed by a Dunn's post-hoc test. The bars bearing the same letters indicate values that are not significantly different at the 5% level. A separate analysis was conducted for (■) *Wasmannia auropunctata* abundance (regular font) and (□) native ant abundance (italics). Curves indicate the species richness ((○), sum of species collected in each zone, *W. auropunctata* included).

edge and decreased with distance from the edge. This tendency was concordant for the two periods (Fig. 1).

In July 1999, the abundance of *W. auropunctata* was significantly different between zones (Kruskal–Wallis test; $H = 113.84$; d.f. = 6; $P < 0.001$). According to the post-hoc test, the first two zones (0–20 m and 20–40 m) supported significantly more ants than the other zones (Fig. 1a).

In March 2000, the abundance of *W. auropunctata* was also significantly different between the invaded zones (Kruskal–Wallis test; $H = 126.05$; d.f. = 6; $P < 0.001$). *Wasmannia auropunctata* was much more abundant in the first zone (0–20 m) and its population decreased significantly with increasing distance from the forest edge (Fig. 1b).

Impact on native ants

A total of 24 ant species or morphospecies from 14 genera were recorded during the study (Table 1). *Wasmannia auropunctata* was the only introduced species, the others were native or endemic species. The richest subfamily was Myrmicinae (16 species), followed by Ponerinae (five species), Formicinae (two

species) and Dolichoderinae (one species). The richest genus was *Lordomyrma* (five species). As *Pheidole* spp. constituted nearly one-half of the native foragers trapped over the two sampling periods (Table 1), they were numerically dominant in the native ant community.

The abundance and richness of the native ant species was consistently higher in the non-invaded zones (Fig. 1). In invaded plots, *W. auropunctata* represented quantitatively more than 92 and 96%, respectively, of the entire ant fauna in July 1999 and March 2000. The few individuals of native ants collected in the invaded zone belonged to cryptic species such as *Hypoponera pruinosa*, *Hypoponera* sp. A, *Oligomyrmex sodalis* and *Strumigenys* sp.

In July 1999, the abundance of native species was different between the zones (Kruskal–Wallis; $H = 66.74$; d.f. = 6; $P < 0.001$). Post-hoc tests indicated differences between the invaded and the non-invaded areas (Fig. 1). The fourth zone (60–80 m, where the invasion front was located) showed an intermediate native ant abundance. This pattern was also observed in March 2000, with significant differences between invaded and non-invaded zones (Kruskal–Wallis; $H = 87.37$; d.f. = 6; $P < 0.001$).

Table 1. Litter ant species, sampled using pitfall traps, in a New Caledonian rainforest partly invaded by *Wasmannia auropunctata*

Species	Status	1999	2000
Ponerinae			
<i>Hypoponera pruinosa</i> (Emery) 1900	Native	1	0
<i>Hypoponera</i> sp. A	Native	0	5
<i>Leptogenys acutangula</i> (Emery) 1914	Endemic	1	14
<i>Rhytidoponera numeensis</i> (André) 1889	Endemic	13	22
<i>Rhytidoponera versicolor</i> , Brown 1958	Endemic	4	9
Myrmicinae			
<i>Lordomyrma caledonica</i> (André) 1889	Endemic	0	2
<i>Lordomyrma</i> sp. A	Endemic	4	1
<i>Lordomyrma</i> sp. B	Endemic	5	3
<i>Lordomyrma</i> sp. C	Endemic	8	2
<i>Lordomyrma</i> sp. D	Endemic	18	5
<i>Monomorium longipes</i> (Emery) 1914	Endemic	1	0
<i>Monomorium</i> sp.	Native	1	0
<i>Oligomyrmex sodalis</i> (Emery) 1914	Endemic	3	4
<i>Pheidole luteipes</i> , Emery 1914	Endemic	35	63
<i>Pheidole</i> sp. A	Endemic	16	27
<i>Pheidole</i> sp. B	Endemic	4	0
<i>Strumigenys</i> sp.	Native	0	2
<i>Solenopsis papuana</i> , Emery 1900	Native	4	1
<i>Tetramorium</i> sp.	Native	2	2
<i>Vollenhovia</i> sp.	Native	3	0
<i>Wasmannia auropunctata</i> (Roger) 1863	Introduced	403	1513
Dolichoderinae			
<i>Leptomyrme pallens nigriceps</i> , Emery 1914	Endemic	4	5
Formicinae			
<i>Paratrechina caledonica</i> (Forel) 1902	Endemic	6	3
<i>Paratrechina foreli</i> (Emery) 1914	Endemic	7	8

The numbers of foragers collected in July 1999 and March 2000 are given for each species

Differences between the two periods

The overall number of *W. auropunctata* foragers collected in March 2000 (1513 individuals) was much greater than in July 1999 (403 individuals); the population nearly quadrupled. For each zone in the invaded area (i.e. from the edge up to 80 m into the forest), the numbers of *W. auropunctata* foragers differed significantly between the two periods (Table 2).

The native ant species richness was similar, but there was a slight difference in the composition due to the rarity of some species (Table 1). In the non-invaded area, the number of native ants collected increased slightly (a total of 140 individuals were collected in July 1999 vs 178 in March 2000), but there were no significant differences between the two sampling periods (Table 2).

DISCUSSION

Invasive progress and impact on native ants

Related studies have shown that ultramafic soils do not induce an ecological barrier against *W. auropunctata* in New Caledonia, as observed for other invaders (Jourdan 1997b). Indeed, we have shown here that dense, pristine rainforests characterized by these soils are also invaded and that this tramp ant can develop huge populations in these fragile biota. Between the two sampling periods, *W. auropunctata* abundance increased strongly while that of native ants was stable in the non-invaded areas. The invasive species therefore demonstrated strong demographic growth while the abundance and the richness of native ants was severely reduced in invaded zones. This is consistent with previous studies conducted in other invaded areas worldwide, including the Galapagos archipelago, other New Caledonian areas and Vanuatu (Clark *et al.* 1982; Lubin 1984; Jourdan 1999; Jourdan *et al.* 2002). The

novelty of the present study is that it is the first assessment of such an invasion and extermination of native species in an undisturbed rainforest. As our sampling design ran from a forest edge, one could argue that the pattern of native ants could result from edge-related environmental gradients. According to Carvalho and Vasconcelos 1999), in central Amazonia, distance to forest edge significantly affected epigaeic ant species composition (up to 200 m from the edge). However, other evidence suggests that the observed pattern is related to the spread of *W. auropunctata*. The dominant *Pheidole* spp. have been recorded from other rainforest edges (unpubl. data from winkler extractors). Also, the number of native species recorded in invaded plots is extremely low (Fig. 1).

Though we did not use baits in this study, the ability of *W. auropunctata* to exclude other ants from food resources has already been shown in the Galapagos (Meier 1994) and in sclerophyll habitat in New Caledonia (Delsinne *et al.* 2001).

The competitive success of *W. auropunctata* in the New Caledonian rainforest is in strong contrast to that observed in its original range, where it never dominates the ant community (Levings & Franks 1982; Tennant 1994). Using tuna baiting to survey ant communities in primary tropical forests in Costa Rica and Panama, Tennant (1994) concluded that *W. auropunctata* is able to coexist with overlapping ant species with similar dietary requirements and foraging behaviours. In a tropical forest with diverse nesting and food resources, *W. auropunctata* may be able to exploit many of these resources while leaving enough food and nest sites for other ant species in the area. According to our results, this is not the case in New Caledonia. This might be due to the huge populations of this intruder, which do not allow other species to coexist in the conditions of low trophic production of the ultramafic rain forest.

In rainforests within the natural range of *W. auropunctata*, Tennant (1994) found that several ant species, particularly of the genus *Pheidole*, compete successfully against *W. auropunctata* and may help keep its population densities low. In contrast,

Table 2. Results of a Wilcoxon signed rank test (W) to compare the abundance of *Wasmannia auropunctata* and native species between July 1999 and March 2000

Distance from the forest edge (m)	<i>Wasmannia auropunctata</i>			Native species		
	W	No. traps per zone	P	W	No. traps per zone	P
0–20	385.0	30	**	–3	30	NS
20–40	212.0	24	**	1	24	NS
40–60	276.0	24	**	–2	24	NS
60–80	169.0	24	*	–13	24	NS
80–100	7.0	24	NS	21.0	24	NS
100–120	0.0	24	NS	78.0	24	NS
120–135	0.0	18	NS	24.0	18	NS

The 0–100 m zone was invaded by *W. auropunctata* whereas the 100–135 m zone was not. NS \geq 0.05; * $P \leq$ 0.05; ** $P <$ 0.001.

in the New Caledonian rainforest the presence of *W.auropunctata* leads to the extermination of all native ants, including *Pheidole* spp., the numerically dominant native species. To date, local ants seem unable to regulate the population densities of *W.auropunctata* through competition.

Mechanisms involved in native ant species displacement by *Wasmannia auropunctata*

Generally, in multispecies systems, the level of repulsion observed between co-occurring species should be directly proportional to the amount of overlap in resource use (Levings & Traniello 1981). *Wasmannia auropunctata* is a true generalist ant (Ulloa-Chacón & Cherix 1990; Tennant 1994; Jourdan 1999) in its feeding habits (Clark *et al.* 1982), the choice of nests sites (Young 1986; Blüthgen *et al.* 2000) and its temporal activity (Clark *et al.* 1982). These ecological attributes induce potential competition with a wide number of native ant species in the forest studied. This competitive ability is reinforced by the ant's unicoloniality. Although the mechanisms by which *W.auropunctata* displaces native ants of this ultramafic forest remain undetermined, Delsinne *et al.* (2001) have shown its ability to monopolize tuna baits in a sclerophyll forest. Although *W.auropunctata* does not use repellent substances to displace native ants (Le Breton *et al.* 2002), competition may play a major role and predation on other ant species should not be ruled out. The success of *W.auropunctata* can be related to the tramp species' attributes coupled with more specific characteristics such as a highly poisonous sting, a good recruitment ability, the small size of the workers and its large population density. The success of *W.auropunctata* in disrupting and displacing native ants in New Caledonia is similar to that of other tramp species, such as *P.megacephala* in Australia (Hoffman *et al.* 1999; Vanderwoude *et al.* 2000), *L.humile* in northern California (Human & Gordon 1999) and the fire ant *S.invicta* in the southern United States (Porter & Savignano 1990; Gotelli & Arnett 2000). This reinforces the idea of common evolutionary traits in tramp species, which leads to a higher competitiveness in new environments.

The characteristics of the New Caledonian native ants might also play a role. This fauna is characterized by a high level of endemism and many primitive traits (Taylor 1987; Jourdan 2002). As stated by Wilson (1961) for Melanesian ant assemblages, these traits may involve a lack of competitiveness, probably a key factor explaining the lack of resistance against new colonisers.

The exclusion of native ant species was observed even at low densities of *W.auropunctata* (Fig. 1). This may be due to the high level of aggressiveness of the

invader and its dominance at food sources, as observed in northern California during interactions between *L.humile* (the Argentine ant) and native species (Human & Gordon 1999). Competitive replacement appears to be the primary mechanism behind the extirpation of native ant faunas. The few native ant species that persist in invaded areas may be those that forage in different strata. A similar process was described for the Argentine ant in California (Ward 1987).

This study also shows that *W.auropunctata*, like other tramp species, are able to invade undisturbed ecosystems. Given the key ecological role of ants (Wilson 1987; Hölldobler & Wilson 1990), the massive disruption wrought by these invaders on the native ant community is likely to have ecosystem-wide repercussions. Further studies of the impact (including a time series at advancing fronts), as well as detailed behavioural studies, are urgently needed to improve our understanding of invasive ant success.

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