

Ecologically heterogeneous populations of the invasive ant *Wasmannia auropunctata* within its native and introduced ranges

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Abstract. 1. The biology of most invasive species in their native geographical areas remains largely unknown. Such studies are, however, crucial in shedding light on the ecological and evolutionary processes underlying biological invasions.

2. The present study focuses on the little fire ant *Wasmannia auropunctata*, a species native to Central and South America that has been widely introduced and which has become invasive throughout the tropics. We characterise and compare several ecological traits of native populations in French Guiana with those in one of its introduced ranges, New Caledonia.

3. We found ecologically heterogeneous populations of *W. auropunctata* coexisting in the species' native geographical area. First, we found populations restricted to naturally perturbed areas (particularly floodplains) within the primary forest, and absent from the surrounding forest areas. These populations were characterised by low nest and worker densities. Second, we found dominant populations in recent anthropogenic areas (e.g. secondary forest or forest edge along road) characterised by high nest and worker densities, and associated with low ant species richness. The local dominance of *W. auropunctata* in such areas can be due to the displacement of other species (cause) or the filling-up of empty habitats unsuitable to other ants (effect). With respect to their demographic features and ant species richness, the populations of native anthropogenic habitats were to a large extent similar to the invasive populations introduced into remote areas.

4. The results point to the need for greater research efforts to better understand the ecological and demographic features of invasive species within their native ranges.

Key words. Biological invasion, disturbance, ecological traits, native, *Wasmannia auropunctata*.

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Introduction

The successful establishment and spread of species to areas outside of their native range is now considered to be a major contributor to the current ecosystems modifications at the global level (Vitousek *et al.*, 1997; Clavero & Garcia-Berthou, 2005;

Lockwood *et al.*, 2007). The unprecedented extent and frequency of bioinvasions are mainly due to a large increase of human activity. To date, most of the studies conducted on biological invasions have focused on invasive species in their introduced range (Elton, 1958; Holway *et al.*, 2002; Williams & Smith, 2007). Moreover, the classical conceptual frameworks used in invasion ecology usually consider the native range of an introduced species as a homogeneous area, both in terms of habitat and the biological features of the species (Colautti & MacIsaac, 2004; Falk-Petersen *et al.*, 2006; Richardson & Pysek, 2006). However, more and more authors agree on the fact that studies about the biology of invasive species within their native range are required (Sakai *et al.*, 2001; Bossdorf *et al.*, 2005; Pedersen *et al.*, 2006), and that native areas are not necessarily biologically homogeneous habitats occupied by ecologically homogeneous populations, from which introduced populations are drawn at random (e.g. Winkler *et al.*, 2008). This recent change of focus within the field of invasion biology, towards a more integrative approach which largely includes populations within the native range of the invasive species, is of fundamental importance. In agreement with this, some authors have recently presented generic conceptual frameworks that suggest that the ecological and/or evolutionary changes underlying biological invasions might occur within the native range of the introduced species (Facon *et al.*, 2006; Lee & Gelembiuk, 2008; Valéry *et al.*, 2008).

Ants occupy a central place in the functioning of ecosystems, because of their ubiquity and the relationships they have developed with fauna and flora. Several studies have highlighted the major direct and indirect ecological consequences of ant invasions (Holway *et al.*, 2002; O'Dowd *et al.*, 2003). Here we focus on the little fire ant, *Wasmannia auropunctata* (Roger, 1863) (Hymenoptera: Formicidae), one of the few ant species listed as one of the 100 'world's worst' invaders (Lowe *et al.*, 2000). Native to Central and South America, this ant has been introduced throughout the tropics including several West African countries, and Caribbean and Pacific islands (Wetterer & Porter, 2003). Introduced populations of *W. auropunctata* have had a major impact on the ecosystems in these areas by competing with and displacing most of the native ant species, and by preying on other invertebrates (Lubin, 1984; Le Breton *et al.*, 2003; Walker, 2006). In its native range, *W. auropunctata* has been recorded as a common species with opportunistic nesting and feeding habits (Tennant, 1994; de la Fuente & Marquis, 1999; Hahn & Wheeler, 2002). It nests mainly on the ground and in the leaf litter, but colonies can also shelter in myrmecophytic plants, epiphytes, and in the canopies of plantation trees (Delabie, 1990; Tennant, 1994; Dejean *et al.*, 1995; Blüthgen *et al.*, 2000; Alvarez *et al.*, 2001; Armbrrecht *et al.*, 2001; Armbrrecht & Ulloa-Chacon, 2003). The demographic and ecological features of *W. auropunctata* populations in their native geographical range remain, however, poorly known.

The aim of the present study was to conduct a detailed survey of several ecological and demographic features of the populations of the little fire ant in its native geographical range (i.e. nest, worker, brood and queen densities, as well as other ant species richness), and to compare these features to those

displayed by introduced invasive populations. We more specifically addressed the following questions: are there ecologically distinct populations of *W. auropunctata* within its native range? Are there native populations of *W. auropunctata* that are similar, with respect to the above features, to the invasive populations introduced into remote areas? To answer these questions, we made a census of the species in various habitats of French Guiana and investigated the nest density, worker, brood, and queen densities, as well as other ant species richness of several native populations of *W. auropunctata* located in anthropogenic and natural areas. To determine whether and how native populations are different from introduced ones, these results were compared with those from a similar survey we also performed on two introduced invasive populations located in natural habitats of the island of New Caledonia.

Materials and methods

Study sites

The part of the study that was carried out in the native range of *W. auropunctata* was conducted in the area around the Petit Saut hydroelectric dam reservoir in French Guiana (4°59'N, 53°08'W) between 2002 and 2004 (Fig. 1). During an extensive preliminary census in various habitats of French Guiana, two of the authors (JO and JLB; survey achieved in 2001) have found that *W. auropunctata* was only present in anthropogenic habitats (i.e. in areas that have undergone an anthropogenic influence) and, to a lesser extent, in particular natural habitats, especially floodplains along creeks. We hence focused the present survey on several anthropogenic and natural habitats that were representative of the actual distribution range of the species in its native area. The studied anthropogenic areas consisted of two secondary forest fragments and a forest edge located along the paved road leading to the Petit Saut dam (see Fig. 1). This road was built between 1988 and 1989 to allow access to the dam site. The natural habitats consisted of floodplains along creeks and the surrounding forests located along a dirt road running perpendicular to the paved one. The objective of this study was not to determine the factors that predict the presence/absence of *W. auropunctata*, but to characterise the ecological and demographic traits of native populations, as well as the ant species diversity in relation to the presence of *W. auropunctata*. Therefore, the chosen sampled sites were not necessarily spatially independent (i.e. not randomly selected).

New Caledonia was invaded after a single introduction of *W. auropunctata* around 40 years ago (Foucaud *et al.*, 2006). The two survey sites in New Caledonia (Pindai: 21°21'S, 164°57'E and the *Rivière Bleue* National Park: 22°6'S, 166°40'E; Fig. 1) were both located in areas recently invaded by *W. auropunctata*. Pindai is dominated by sclerophyllous forest remnants and the presence of *W. auropunctata* was first noted in 1991. The *Rivière Bleue* National Park is dominated by evergreen forests, and was invaded between 1995 and 1997 (Jourdan, 1999). Both sites can be considered as natural habitats.

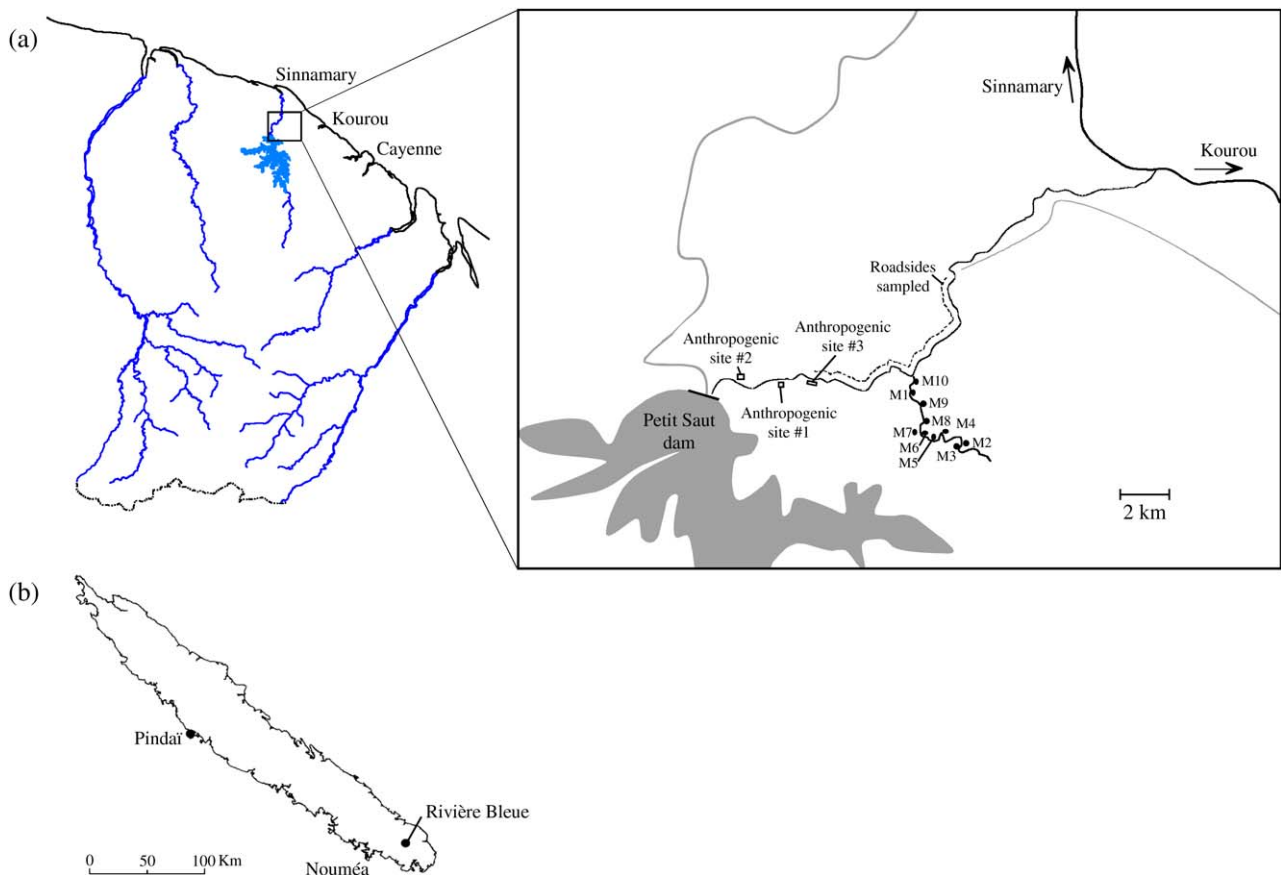


Fig. 1. Sites sampled for ecological and demographic surveys in French Guiana (a) and in New Caledonia (b). In French Guiana, M1 to M10 refer to the natural sites located on floodplains in the primary forest. The roadsides sampled include 20 sites (see Materials and Methods for details). The anthropogenic sites 1, 2 and 3 correspond to two secondary forest fragments and one forest edge, respectively. In New Caledonia, Pindaï and Rivière Bleue correspond to fragments of sclerophyllous and evergreen forests, respectively.

Occurrence and transition between anthropogenic and natural habitats

We sampled a total of 20 sites at intervals of 500 m located over 10 km along the paved road leading to the Petit Saut dam (Fig. 1). The frequency of ant occurrence was monitored at each site along two parallel transects 20 m apart, starting from the roadsides to 50 m inside of the natural forest (total = 40 transects). Each transect passed through three types of habitats, namely: 'open land', which is the herbaceous strata closest to the road; 'forest edge', which is a 20-year-old pioneer vegetal formation that grew after the road was constructed; and the 'natural forest'. Each type of habitat varied in the degree to which it was disturbed, canopy cover and floristic composition. Ten baits were placed on the ground at 5-m intervals along each transect. The baits consisted of a combination of bits of tuna tinned in oil, honey, and cookie crumbs known to attract a wide range of ant species (Human & Gordon, 1999). One hour later, we assessed the number of workers (all ant species combined) foraging on the baits, and we also searched for *W. auropunctata* workers around the baits during 2 min.

The surveys of *W. auropunctata* in natural areas were conducted on floodplains along creeks and in the surrounding forest.

These sites were selected because (1) our preliminary census did not record any *W. auropunctata* populations outside this particular type of natural habitat, and (2) the *W. auropunctata* colonies recorded were unlikely to have been introduced into these areas through human activity. In total, 10 sites distributed along 6 km of a dirt road were sampled (Fig. 1). At each site, two transects were set up, one within the floodplain and one in the surrounding forest. As noted above, 10 baits were placed on the ground at 5-m intervals over each transect, and we assessed the number of workers foraging on the baits after 1 h. In addition, we placed baits on the trunks of any tree with a diameter greater than 10 cm found in each transect ($n = 387$ and 245 on floodplains and in the forest, respectively). Finally, epiphytes ($n = 223$) located up to 3 m in height in the transects along the floodplains were inspected for the presence of ant colonies. No epiphyte was observed at this height in the surrounding forest.

Demographic features of the native and introduced populations

We recorded the number of nests, queens, and workers, as well as broods per m² in the populations located in anthropogenic

areas in French Guiana and in New Caledonia. In both cases, the sampling protocol was the same and consisted of exhaustively sampling all of the *W. auropunctata* nests in 1 m² of leaf litter. The sampled 1 m² quadrats were separated by minimum intervals of 5 m. All of the nests found were subsequently stored in ethanol, or frozen and the numbers of individuals and brood counted. Three human-disturbed sites (two secondary forest fragments and one forest edge) were sampled in French Guiana (anthropogenic sites 1, 2, and 3 in Fig. 1) and two natural sites (one evergreen forest fragment and one sclerophyllous forest fragment) in New Caledonia. Twenty 1 m² quadrats were sampled in each of the two Guianian secondary forest fragments, 23 in the forest edge and 40 in each of the two New Caledonian forest fragments.

In the natural sites we studied in French Guiana (i.e. floodplains of the primary forest), we could not use the previous method due to the low population densities (see Results). We therefore roughly estimated the nest densities of *W. auropunctata* by using count data collected on the above-mentioned transects in the floodplains, as well as on nine other transects that we set up in the same sites to collect entire nests of *W. auropunctata*. For this estimation, we assumed that each bait could potentially attract workers from any nest located up to 2 m away. This assumption derives from the harvesting of *W. auropunctata* colonies that we carried out in floodplains, in order to find the nests of workers recruited on baits by following their recruitment trails.

Ant species richness in relation to *Wasmannia auropunctata*

The potential relationship between the presence of *W. auropunctata* and the diversity of the ant community in anthropogenic areas of French Guiana was evaluated throughout a detailed study of the roadside areas. The 40 transects examined along roadsides (see above and Fig. 1) were divided into three main categories according to the occurrence and abundance of *W. auropunctata*: high density, low density, and absence. High density areas correspond to transects where hundreds of *W. auropunctata* were dominating several baits, while in low density areas, only one or two baits were occupied by less than 100 workers. We focused only on the baits deposited in the areas from the open land to the forest edge, because such areas turned out to be a main habitat for *W. auropunctata* (see Results for details). For each transect, the ant species diversity was noted and the number of species other than *W. auropunctata* was compared for each category of *W. auropunctata* occurrence (i.e. high density, low density, and absent) using a one-way ANOVA followed by a Tukey's *post-hoc* test for multiple comparisons.

We also assessed in greater detail the diversity of the ant species foraging on baits in the leaf litter at one site dominated by *W. auropunctata* (anthropogenic site 1; Fig. 1). The baits were deposited along 10 transects separated from each other by a distance of 5 m and running perpendicular to the forest edge. For each transect, nine baits were placed on the ground (one every 5 m). This grid arrangement allowed us to obtain precise data on the distribution of the ant community (including *W. auropunctata*) from the forest edge to the inside of the forest. We monitored the number of individuals from each ant species on each bait after

5, 30, and 60 min. The genus of heterospecific workers present on the baits was also determined.

Results

Census of native populations in anthropogenic and natural areas

In French Guiana, *W. auropunctata* was commonly observed along roadsides as it was detected in 17 out of 20 (i.e. 85%) of the sampled sites. Workers were more frequent in open habitats (mean \pm SE: $41.3 \pm 47.5\%$ of the baits) than in the secondary forest ($29.8 \pm 28.5\%$ of the baits) and almost absent inside of the forest ($3.1 \pm 6.1\%$ of the baits; Fig. 2). The frequency of baits monopolised by *W. auropunctata* was characterised by a variance among the sites sampled along roadsides, which considerably decreased from the road to the forest.

The surveys conducted in natural areas underlined the rarity of the little fire ant in the primary forest, including that surrounding floodplains along creeks (absent on the ground and on 0.4% of the baits on tree trunks; Table 1). We found *W. auropunctata* to be almost strictly confined to floodplains along creeks, which correspond to areas naturally perturbed by temporary flooding events during the rainy season. Workers were indeed recorded in 9 out of 10 of the floodplains sampled either on baits on the ground or on the tree trunks, or nesting inside of the root clusters of epiphytes. Overall, this species has been recorded in 17% of

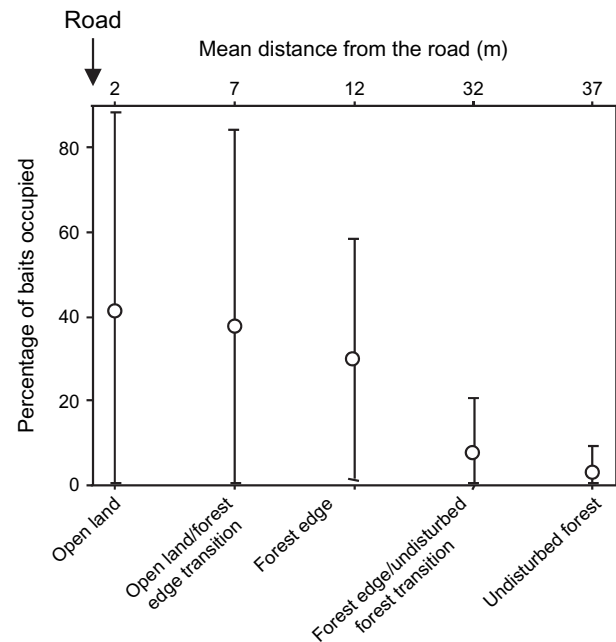


Fig. 2. Percentage (\pm SE) of baits monopolised by *Wasmannia auropunctata* along roadside transects according to the type of habitats. Data were pooled from the 17 sampled sites in which the species was detected and the mean distance from the road to each type of habitat is indicated.

Table 1. Percentage of occurrence of *Wasmannia auropunctata* and other ant species (all pooled) on baits deposited on the ground and on tree trunks, or nesting in the root clusters of epiphytes located up to 3 m in height in primary forests of French Guiana. No epiphytes were recorded at this height in the surrounding forest. Note that the sum of the percentages can be higher than 100% because of cases of *Wasmannia auropunctata* and other ant species sharing the same bait or epiphyte.

	Floodplains				Surrounding forest			
	<i>Wasmannia auropunctata</i>	Other ant species	Empty	<i>n</i>	<i>Wasmannia auropunctata</i>	Other ant species	Empty	<i>n</i>
Ground	17	82	8	100	0	87	13	100
Tree trunks	6.5	60.5	33.8	387	0.4	55.9	43.7	245
Epiphytes	8.5	65.0	26.9	223	—	—	—	—

the baits placed at the ground level, in 6.5% of the baits placed on the tree trunks, and nesting in 8.5% of the epiphytes (Table 1).

Demographic structure of the native and introduced populations

Within the native geographical range of *W. auropunctata*, we found two types of populations characterised by a substantially different demographic structure. First, the natural Guianian forests were occupied by low density populations (ca 0.014 nest m⁻²). Second, the anthropogenic sites were occupied by much higher density populations (>100 times higher densities: mean \pm SD: 2.4 ± 1.8 , 3.8 ± 2 and 4.6 ± 3.6 nests m⁻² in the anthropogenic sites 1, 2, and 3, respectively). Both types of native populations were, however, found at a significantly lower density than the introduced population (New Caledonian sites: 8.3 ± 3.4 and 19.6 ± 9.3 nests m⁻² in the evergreen and sclerophyllous forests, respectively; Fig. 3a).

The compositions of the nests also varied between the different areas and forest types sampled. In the two New Caledonian forest areas, the number of queens per m² was high, although extremely variable (mean \pm SD: 35.7 ± 24.8 and 90.0 ± 81.9 queens m⁻² in the evergreen and in the sclerophyllous forests, respectively), and significantly higher than in the three anthropogenic sites in French Guiana (2.2 ± 2.5 , 0.9 ± 1.4 , and 1.8 ± 2.4 queens m⁻² in the anthropogenic sites 1, 2, and 3, respectively; Fig. 3b). In New Caledonia, the proportion of nests sheltering at least one queen was also high and linked to the high number of queens per m² (Fig. 4). Nevertheless, this proportion of queenright nests was not significantly higher in the New Caledonian sclerophyllous forest fragment than in most of the areas sampled in French Guiana.

It is worth stressing that native populations in the anthropogenic sites display worker densities similar to those of introduced populations in New Caledonia. The numbers of workers and brood per m² were mostly similar between anthropogenic native and introduced sites (Fig. 3c,d). These worker densities were, however, distributed differently in the two types of populations: fewer, but more populous nests for the native populations of anthropogenic sites, versus numerous, but smaller, nests in the introduced population of New Caledonia.

Ant species richness in presence or absence of *Wasmannia auropunctata*

In French Guiana, whereas the little fire ant was commonly recorded in the open land along roadsides to the forest edge, it was found to be at high (absolute) density in only 4 of the 40 transects. When present at high density, *W. auropunctata* workers monopolised almost all of the baits at all times, and a total of only eight other species (*Crematogaster limata* Smith, F., *Cr. tenuicula* Forel, *Odontomachus haematodus* L., *Pachycondyla* sp., *Pheidole* spp., *Pseudomyrmex terminarius* Smith, and *Solenopsis* sp.) were occasionally recorded. In contrast, a considerably larger ant diversity was systematically noted on the baits placed in the transects where *W. auropunctata* was present at low density (21 species in total), or absent (36 species). A one-way ANOVA shows that the mean number of species (excluding *W. auropunctata*) was significantly different between the three levels of occurrence (2.0, 3.9, and 4.6 for transects with *W. auropunctata* at high density, low density and absent, respectively; $F_{2,37} = 4.09$, $P = 0.025$). The significant positive association between the presence of *W. auropunctata* and the decrease of ant species richness was only due to the differences between the 'high density' and 'absent' transects (Tukey's *post-hoc* test, $p_{\text{high density vs absent}} = 0.02$, $p_{\text{high density vs low density}} = 0.14$, and $p_{\text{low density vs absent}} = 0.51$).

The relationship between the presence of *W. auropunctata* and ant species richness was further studied in greater detail in a disturbed Guianian site. *Wasmannia auropunctata* was found to completely dominate a zone ranging from the edge to the first 20 m of the secondary forest (Fig. 5a). Numerous *W. auropunctata* workers were already present at the baits even after only 5 min. We did not detect any other ant species on any of the baits located 0, 5 and 10 m from the edge, and only a few heterospecific workers were noted on the baits located 15 and 20 m away (Fig. 5b). The abundance of *W. auropunctata* was found to abruptly and drastically decrease on baits located 25 m away, and no workers were recorded further than 30 m away. Concomitantly, the abundance of foraging workers from other ant species increased considerably on baits located 25 to 40 m from the forest edge. The heterospecific workers recorded on the baits mainly belonged to the genera *Pheidole*, *Solenopsis*, *Crematogaster*, and *Camponotus*. This striking pattern held true for baits examined regardless of the time interval (i.e. after 5, 30, and 60 min).

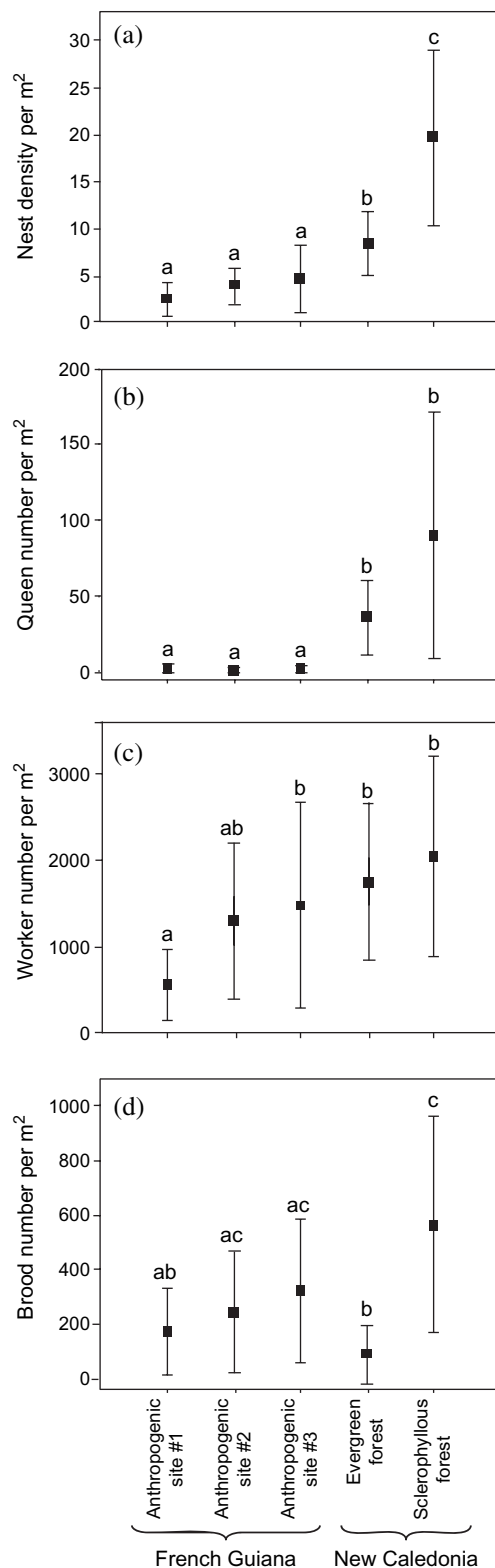


Fig. 3. Differences (\pm SD) in nest densities (a) and in the numbers of *Wasmannia auropunctata* queens (b), workers (c), and brood (d) in three anthropogenic areas of French Guiana and two invaded sites in New Caledonia (surface unit = 1 m²). The anthropogenic sites 1 and 2 in

Discussion

Ecologically and demographically distinct populations within the native range

This study highlights the occurrence of two distinct types of native *W. auropunctata* populations. First, in primary forest areas we found non-dominant *W. auropunctata* populations, that are characterised by low nest and worker densities, comparable to densities observed in primary forest areas in Panama (0.05–0.13 nest m⁻², Levings & Franks, 1982). These populations are, at least in our study area, restricted to the floodplains of creeks. *Wasmannia auropunctata* was indeed found to be virtually absent in the surrounding forest, a result in agreement with a preliminary census study achieved by some of the authors. Second, within anthropogenic habitats, we found populations that dominate large areas with nest and worker densities more than 100 times higher than in the populations of floodplains in the primary forest. All of these native populations, whether dominant or not, have been confirmed through the analysis of their morphological characters to belong to the same species (J. H. C. Delabie, unpublished results). Consistently, studies using microsatellites and mtDNA genetic markers did not show any monophyletic clustering of dominant versus non-dominant populations (Foucaud *et al.*, 2007; J. Foucaud, unpublished results). With respect to the dominance of *W. auropunctata* on other ant species in anthropogenic habitats, it is worth pointing that our survey does not allow us to discriminate between two (not necessarily exclusive) explanations: the local dominance can indeed be due to the displacement of other species (cause) or the filling-up of empty habitats unsuitable to other ants (effect). Temporal surveys based on particular experimental designs, such as those used on the Argentine ant by Suarez *et al.* (1998), would be necessary to discriminate between these two explanations.

Interestingly enough, dominant populations of the little fire ant located in anthropogenic habitats of the native range were found to be similar, with respect to worker density and low ant species richness, to the introduced New Caledonian populations (see also Le Breton *et al.*, 2005) and to those highlighted by most studies on neotropical ant diversity in anthropogenic ecosystems invaded by *W. auropunctata* (Armbrecht & Ulloa-Chacon, 2003; Wetterer & Porter, 2003).

Wasmannia auropunctata is a disturbance specialist in its native range

The fact that *W. auropunctata* is known as a 'disturbance specialist', as defined by Majer and Delabie (1999) for populations from anthropogenic areas, seems to also apply to the populations from natural areas. Low density populations are restricted to the floodplains along creeks and virtually absent from the surrounding

French Guiana were two secondary forest fragments and the anthropogenic site 3 was a forest edge. Symbols bearing the same letters indicate values that are not significantly different at the 5% level of significance (Mann-Whitney *U*-test followed by a Bonferroni correction).

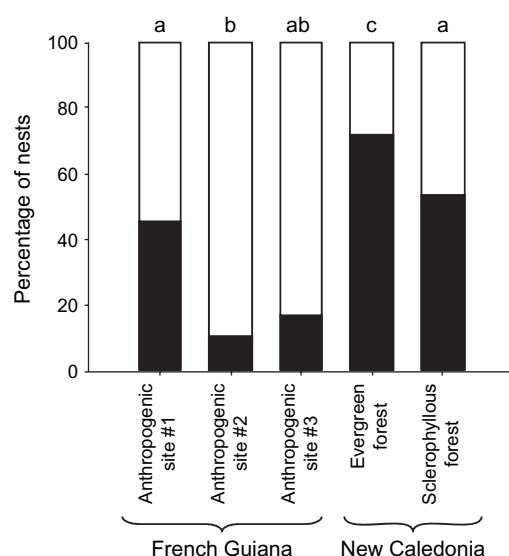


Fig. 4. Comparison between the proportions of queenright and queenless nests in three anthropogenic areas of French Guiana and two invaded sites in New Caledonia. Black and white areas of the bars represent the percentages of queenright and queenless nests, respectively. The anthropogenic sites 1 and 2 in French Guiana were two secondary forest fragments and the anthropogenic site 3 was a forest edge. Bars bearing the same letters indicate values that are not significantly different at the 5% level of significance (χ^2 test followed by a Bonferroni correction).

primary forest. This suggests the existence of ecological factors enabling *W. auropunctata* colonies to settle on floodplains in the primary forest. The regular floods that occur in these areas during the rainy season lead us to consider them as naturally disturbed sites. Even if the level of disturbance is low and transient compared to the human-caused disturbances associated with anthropogenic sites, this might favour the settlement and development of *W. auropunctata* populations noticeably by lowering the intensity of interspecific competition. Biotic factors seem indeed to better explain the pattern of occurrence of the little fire ant in the natural areas than do abiotic factors. We found no or only small differences in climatic conditions, as indicated by temperature and humidity measurements, between the floodplains and the surrounding forest (see Supporting Information Figures S1, S2, and S3). On the other hand, we found strong significant differences in maximal daily temperature and minimal daily humidity, as well as in daily variation between natural (i.e. floodplains or surrounding forest) and anthropogenic habitats (see Supporting Information Figures S1, S2, and S3). These differences translate into a globally warmer, drier and more variable climate in anthropogenic habitats than in natural habitats. These major differences in abiotic factors might explain at least partly the ecological distinctiveness between *W. auropunctata* populations of natural versus anthropogenic habitats.

The expression or non-expression of dominance features by *W. auropunctata* within its native geographical range seems to be dependent on a combination of both abiotic and biotic factors. The absence of competitors in the pioneer formations created by human disturbance (e.g. in forest edges, plantations) may have

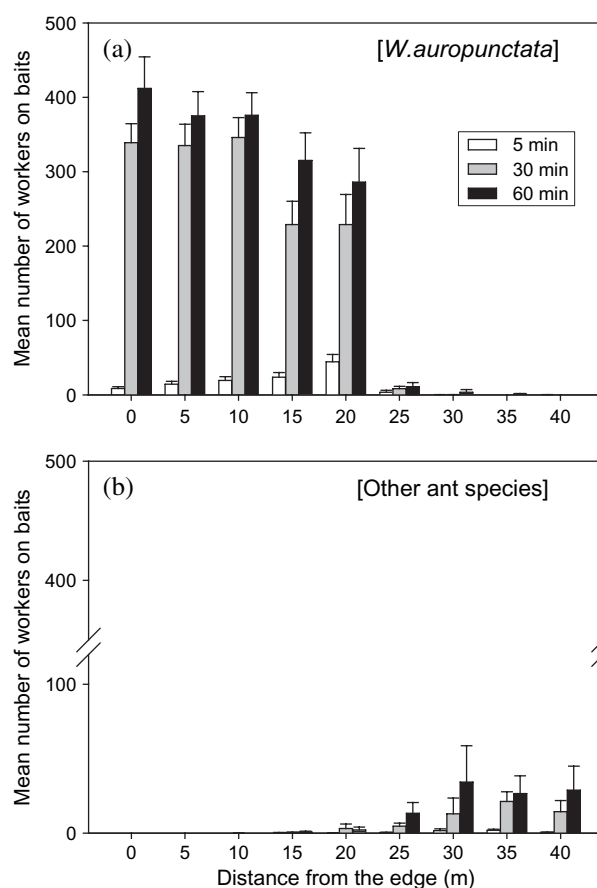


Fig. 5. Mean number of workers (\pm SE) of *Wasmannia auropunctata* (a) and other ant species (all pooled) (b) in an area of secondary forest in French Guiana. Workers were recorded after 5, 30, and 60 min on baits located at different distances from the edge of the forest.

favoured the settlement and development of high density populations of *W. auropunctata*. Consequently, disturbance-specialist traits, associated with other characteristics, such as the absence of clear colonial boundaries favouring uniclonality and great flexibility in its nesting and food requirements, are of importance in the consideration of the invasive success of *W. auropunctata* (Chapman & Bourke, 2001). Interestingly, similar ecological patterns have also been noted in other invasive ant species, *Linepithema humile* Mayr, *S. invicta* Buren, and *Lasius neglectus* Van Loon, Boomsma & Andr  sfalvy (Pedersen *et al.*, 2006; Tschinkel, 2006; Bolger, 2007; Calcaterra *et al.*, 2008; Cremer *et al.*, 2008; Suarez & Tsutsui, 2008; Ugelvig *et al.*, 2008). Our study and previous studies focusing on invasive ant species, thus seem to illustrate that adaptation to disturbance within native habitats might be one of the key factors in the invasive success of many species, as recently pointed out by Lee and Gelembiuk (2008).

Conclusion

Our results point to the need for greater research efforts to better understand the ecological and demographic features of invasive

species within their native ranges. Further studies are needed to assess whether local adaptations or phenotypic plasticity response to different ecological conditions are needed to explain the dominance of *W. auropunctata* populations in anthropogenic habitats within its native range. We are presently studying dominant and non-dominant native, as well as introduced populations of *W. auropunctata* to decipher the relative contributions of ecological, genetic, and behavioural traits in the emergence of native dominant and introduced invasive populations of this major pest species.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. Raw distributions of temperature and humidity records in natural and anthropogenic sites in French Guiana.

Figure S2. Statistical tests on the distributions of longitudinal measures of mean minimum and maximum values of temperature (A) and humidity (B) recorded in one anthropogenic and two natural sites in French Guiana.

Figure S3. Statistical tests on the distributions of longitudinal measures of daily variation in temperature (A) and humidity (B) recorded in one anthropogenic and two natural sites in French Guiana.

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Supplementary figure S1. Raw distributions of temperature and humidity records in natural and anthropogenic sites in French Guiana.

We recorded the temperature and humidity at the soil level (one coupled measure every 20 min from April 2006 to January 2008) to characterize the abiotic conditions faced by *W. auropunctata* populations in three natural sites (two flood plains and one surrounding primary forest) and two anthropogenic sites (secondary forest for site #1 and open land on the roadside for site #2).

Supplementary figure S2. Statistical tests on the distributions of longitudinal measures of mean minimum and maximum values of temperature (A) and humidity (B) recorded in one anthropogenic and two natural sites in French Guiana.

The sites and raw data are those illustrated in Figure S1A, S1C and S1E. The three sites we compared were chosen because their corresponding recording periods overlapped for a large number of days (290 consecutive days). The variables temperature and humidity were considered separately and summarized through one value per day (minimum and maximum values). Histograms represent mean minimum (gray bars) and maximum (white bars) values ($\pm 1.96SE$). The studied sites were tested by pair using the Wilcoxon signed rank test. We have chosen the later non parametric test although the data, consisting of temporal records, were unlikely to be independent within each site. This is because not any non-parametric comparison test allows taking into account intra-sample dependence. Taking into account the intra-sample dependence of our data would imply to estimate the dependence structure of the data assuming a non-realistic distribution of the data (e.g. Normal distribution). Symbols bearing the same letters indicate values that are not significantly different at the 5% level of significance.

Supplementary figure S3. Statistical tests on the distributions of longitudinal measures of daily variation in temperature (A) and humidity (B) recorded in one anthropogenic and two natural sites in French Guiana.

We computed standard deviations for each day to summarize daily variation in temperature and humidity, considering separately the variables temperature and humidity. The sites and raw data are those illustrated in Figure S1A, S1C and S1E. The three sites we compared were chosen because their corresponding recording periods overlapped for a large number of days (290 consecutive days). Histograms represent mean daily standard deviations in temperature (A) and humidity (B) ($\pm 1.96SE$). The studied sites were tested by pair using the Wilcoxon signed rank test. We have chosen the later non parametric test although the data, consisting of temporal records, were unlikely to be independent within each site. This is because not any non-parametric comparison test allows taking into account intra-sample dependence. Taking into account the intra-sample dependence of our data would imply to estimate the dependence structure of the data assuming a non-realistic distribution of the data (e.g. Normal distribution). Symbols bearing the same letters indicate values that are not significantly different at the 5% level of significance.

