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Niche opportunity and ant invasion: the case of *Wasmannia auropunctata* in a New Caledonian rain forest

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Abstract: Due to the unbalanced distribution of their fauna and flora, which leads to the creation of a niche opportunities, it is generally accepted that island communities offer weak biotic resistance to biological invasion. In order to empirically test this statement, we compared resource use by ants in the understorey of an undisturbed New Caledonian rain forest recently invaded by the little fire ant, *Wasmannia auropunctata*. We tested the exploitation of (1) food sources by placing baits on all trees with trunks greater than 5 cm in diameter, and (2) nesting sites on two tree species likely to shelter ant colonies. In non-invaded areas, the native ants occupied only 43.6% of the baits after 3 h of exposure, while in invaded areas all the baits were occupied by numerous *W. auropunctata* workers. Similarly, in non-invaded areas only 48.9% of *Meryta coriacea* (Araliaceae) trees and 64.5% of *Bocquillonia* sp. (Euphorbiaceae) sheltered ants, while in invaded areas *W. auropunctata* nested in 92.6–98.3% of these trees. Also, workers attended native Margarodidae (Hemiptera) for which they promoted the development of populations significantly larger than those attended by native ants. Thus native ants appear unable to efficiently exploit and defend several of the available food sources and nesting sites, providing a niche opportunity for an invader like *W. auropunctata*.

Key Words: biological invasions, invasive ants, community ecology, competitive displacement, Hemiptera, Pacific island

INTRODUCTION

Although biological invasions by alien species are a worldwide phenomenon, their impact is particularly significant on isolated islands (Elton 1958, Gremaler et al. 2002, Simberloff 1995). Due to high endemism and extensive adaptive radiation, island communities can be taxonomically disharmonious, with entire families and even higher taxa absent (Carlquist 1974, MacArthur & Wilson 1967). Consequently, islands are often described as offering lower biotic resistance to biological invasions than continental areas by providing a niche opportunity for exotic species (Shea & Chesson 2002, Simberloff 1995), although empirical evidence in support of such statements remains scarce. Because ants proliferate quickly, they are among the most devastating invaders known, and invasions by ants have major ecological consequences (Holway *et al.* 2002, O'Dowd *et al.* 2003). Also, the ability to gain access to and actively exploit plants and the exudates of Hemiptera is basic to the success of the most invasive ant species, whose population explosions are generally accompanied by a population explosion of their attended Hemiptera (Davidson *et al.* 2003, Helms & Vinson 2003, Holway *et al.* 2002, Wetterer & Porter 2003). As a result, they provide a good model for empirically exploring the hypothesis of niche opportunity and the way in which it might play a role in their invasive success.

Here, we focus on *Wasmannia auropunctata* (Roger) or the little fire ant, a tramp species considered to be one of the most ecologically destructive invaders in areas where it has been introduced (Holway *et al.* 2002, Lowe *et al.* 2000). Consequently, its range extends throughout the tropics, including New Caledonia (Jourdan *et al.* 2002), our study area, which is recognized as a unique biodiversity hotspot (Myers *et al.* 2000). Although rich and highly endemic, the New Caledonian ant fauna is characterized by a paucity of arboreal species if compared with other tropical areas, and arboreal ants represent less than 5% of all canopy arthropods (Jourdan & Chazeau 1999, Wilson 1976).

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We hypothesized that in New Caledonia the native arboreal ant community is too scarce to efficiently exploit and defend food sources and nesting sites from the understorey, providing a niche opportunity to an invader such as *W. auropunctata*. We then examined how the latter species exploits these resources in the invaded areas and noted the consequences on the native ant community.

MATERIALS AND METHODS

Our investigation was conducted from January to April 2002 in a pristine rain forest on ultramafic soils in the Rivière Bleue Natural Park in southern New Caledonia. This forest, which is dominated by Myrtaceae and Rubiaceae and exhibits plant endemism reaching 82% (Jaffré & Veillon 1990), began to be invaded by *W. auropunctata* in 1997 (Le Breton *et al.* 2003). In the park, we selected homogeneous forest plots with similar botanical characteristics (structure and composition), some of them invaded by *W. auropunctata*, permitting a comparison with others not yet invaded.

In order to assess the ants' ability to exploit food sources, we conducted baiting experiments by placing a combination of pieces of tinned tuna in oil, honey and cookie crumbs 2 m high on tree trunks (Human & Gordon 1999). In order to have a representative sample of the understorey vegetation, we selected all trees with a trunk diameter greater than 5 cm in both non-invaded and invaded areas (150 and 117 trees, respectively). We recorded the species and number of workers that foraged on the baits and/or were present within a radius of 2 cm. Some individuals were collected for further identification in the laboratory. Baits were monitored after 1 then 2 h in order to evaluate the rate of species replacement (an indication of competition between ants). Given the poor state of taxonomic knowledge of New Caledonian ants, we identified them at the genus level using keys provided by Shattuck (1999) and then we compared the samples with specimens of known species and assigned code numbers to morphospecies (see Table 1). Voucher specimens were deposited at the Institut pour la Recherche et pour le Développement (IRD) in Nouméa.

In order to assess the exploitation of nesting sites, we examined two common understorey plants able to shelter ant colonies. The distribution of the large leaves of *Meryta coriacea* Baill. (Araliaceae) permits dead leaves and debris fallen from the canopy to accumulate, forming hanging soil. The trunks of *Basselinia pancheri* (Brongn. & Gris) Vieill. (Arecaceae), an endemic palm common in the rain forest understorey (Hodel & Pintaud 1998), are sheathed by the axils of dead fronds that form cavities where ant colonies find shelter, as has often been noted in palms (Way & Bolton 1997). All sampled *Meryta* and *Basselinia* were mature and ranged from 1.20 to 3.50 m tall. Using forceps and an aspirator, we gathered specimens from each ant colony from 129 *Meryta* and 107 *Basselinia* in non-invaded areas of the rain forest. The same method was used for 60 *Meryta* and 63 *Basselinia* in the invaded area.

Table 1. List of ant species recorded in the understorey strata of a New Caledonian rain forest. Under baits, + = foragers detected on baits. Under plants, N = species nesting in the studied plants and F = foragers detected on the plants.

Taxa	Baits	Plants: *Meryta coriacea*	Plants: *Basselinia pancheri*
Ponerinae			
Hypoponera sp.	+	N, F	
Rhytidoponera [illegible] Brown		F	F
Myrmicinae			
Crematogaster sp.	+		F
Lordomyrma sp. 1	+		
Lordomyrma sp. 2		F	F
Monomorium [illegible] (Emery)	+	N, F	
Monomorium [illegible] (Emery)			F
Monomorium sp. 1	+		
Monomorium sp. 2	+		
Monomorium sp. 3	+		
Monomorium sp. 4	+		
Monomorium sp. 5	+		
Monomorium sp. 6	+		
Oligomyrmex sodalis (Emery)	+		
Pheidole sp. 1	+		N, F
Pheidole sp. 2	+		
Pheidole sp. 3	+		
Tetramorium sp.		F	F
Vollenhovia sp.	+		N, F
Wasmannia auropunctata (Roger)	+	N, F	N, F
Dolichoderinae			
Iridomyrmex sp.		N, F	N, F
Iridomyrmex sp. 2		N, F	
Leptomyrmex pallens Emery	+	F	F
Formicinae			
Camponotus gambeyi Emery	+	F	
Camponotus [illegible] Emery	+		F
Camponotus sp. 1	+		
Camponotus sp. 2	+		
Polyrhachis [illegible] Forel		N, F	
Polyrhachis [illegible] Emery	+	N, F	N, F
Polyrhachis [illegible] var. [illegible] Emery	+		N, F
Polyrhachis sp. 2		N, F	N, F
Polyrhachis sp. 3	+		

During sampling, we repeatedly observed that *Basselinia* sheltered native Margarodidae or giant scale insects (Hemiptera: Sternorrhyncha) beneath dead fronds. We subsequently assessed their frequencies and densities in 95 and 135 additional palms from the non-invaded and invaded areas, respectively.

For statistical analyses we used Fisher's exact test to compare rates of exploitation between species and a Wilcoxon test was performed to compare the densities of Margarodidae in invaded and non-invaded areas. All tests were performed using Statistica® 5.0 software.

Table 2. Results of baiting experiments performed in a New Caledonian rain forest (percentage of baits occupied). Baits were placed on tree trunks in areas not invaded and invaded by *Wasmannia auropunctata*. Values are percentage of baits occupied.

	After 1 h		After 2 h	
Taxa	Not invaded (N = 350)	Invaded (N = 117)	Not invaded (N = 291)	Invaded (N = 117)
Paratrechina foreli	18.5		52.2	
Monomorium sp. 2	1.1		1.7	
Camponotus sp. 4	0.6		1.4	
Camponotus [illegible]	0.5		1.0	
Monomorium sp. 3	0.6		1.0	
Paratrechina [illegible]	0.3	-	1.0	
[illegible] sp.			0.7	
[illegible]	0.3		0.7	
Monomorium sp. 1		-	0.7	
[illegible] sp.			0.7	
Camponotus [illegible]	<0.3		0.3	
Camponotus sp. 2	-		0.3	
[illegible] sp.			0.3	
[illegible] sp. 1			0.3	
Monomorium [illegible]			0.3	
Monomorium sp. [illegible]	<0.3		0.3	
Monomorium sp. 4			0.3	
Monomorium sp. 6			0.3	
[illegible]	<0.3		0.3	
[illegible] sp. 3	<0.3		0.3	
Pheidole sp. 1	<0.3	-	0.3	
Pheidole sp. 2	<0.3		0.3	
Pheidole sp. 3	<0.3		0.3	
Wasmannia auropunctata		100		100
No ants	75.1	0	46.1	0

RESULTS

In total, 33 ant species belonging to 14 genera and four subfamilies were noted on the baits and sampled plants (Table 1). With the exception of *W. auropunctata*, all the other ant species were native to New Caledonia, the richest genus being *Monomorium* (eight species), followed by *Paratrechina* (five species) and *Camponotus* (four species).

Bait experiments

After 1 h of being installed, only 86 out of 350 baits (24.6%) placed in the non-invaded areas were occupied by ants belonging to 6 genera and 14 species (Table 2). Of the 291 baits remaining after 2 h (the others were robbed by lizards and birds), 157 (54.0%) were occupied by ants belonging to 10 genera and 24 species (comparison between 1 h and 2 h: Fisher's exact-test: FI = 26.04; df = 1; P < 0.001) (Table 2). The presence of the commonest ant species, *Paratrechina foreli*, increased between 1 and 2 h (18.5% and 52.2% of the baits, respectively; Fisher's exact-test: FI = 11.3; df = 1; P < 0.001). The same was true for all the other ant species when pooled (5.5% after 1 h vs. 13.4% after 2 h; Fisher's exact-test: FI = 11.2; df = 1; P < 0.001). When present, *P. foreli* scouts quickly discovered the baits, but the recruitment of nestmates was weak: after 2 h fewer than 20 workers were recruited that then abandoned the baits when the foragers of other species arrived.

In the invaded area, all the baits were discovered by *W. auropunctata* workers within minutes, and rapidly occupied by numerous recruited nestmates (Table 2). No workers from native species were noted on these baits, but foraging *Paratrechina* sp. workers were observed near on a tree trunk. The mean number of *W. auropunctata* workers per bait varied from 55.3 after 1 h to more than 100 after 2 h.

Meryta coriacea and *Basselinia pancheri* as suitable nesting sites for ants

In the non-invaded area, we sampled the colonies of seven ant species sheltering in 48.8% of the 129 *Meryta* studied (Table 3). Ant colonies nested in *Basselinia* significantly more frequently than in *Meryta* (64.5% of the 107 palm trees sheltered ants belonging to six species; Fisher's exact-test: FI = 5.81; df = 1; P < 0.05; Table 3). In both cases, *P. foreli* was the commonest species, followed by *Paratrechina* sp. 1; other species were rare and mostly represented by foraging workers (Table 1). We noted the presence

Table 3. Occupation by ants of the palm tree *Basselinia pancheri* (Arecaceae) and the trash basket plant *Meryta coriacea* (Araliaceae) in New Caledonian rain forest areas invaded and not invaded by the invasive little fire ant *Wasmannia auropunctata*. Values are percentage of plants occupied.

Taxa	*Basselinia pancheri*		*Meryta coriacea*	
	Not invaded (N = 101)	Invaded (N = 63)	Not invaded (N = 129)	Invaded (N = 60)
Hypoponera sp.		–	0.8	
Rhytidoponera sp. 1	3.0	–	0.8	
Rhytidoponera sp. 2			0.8	
Monomorium longipes			0.8	
Paratrechina caledonica			3.1	
Paratrechina foreli	40.6		26.7	
Paratrechina foreli nigriventris	3.0			
Paratrechina sp. 1	25.2	–	14.7	
Pheidole sp. 1	1.0			
Tetramorium sp.	0.8	–	–	
Wasmannia auropunctata		92.1		98.3
No ant present	16.8	7.9	[illegible]	1.7

of Margarodidae on 24.2% of the sampled *Basselinia*, resulting in a mean number ± SE of 2.9 ± 1.4 individuals per tree attended by native ants.

We did not observe any native ant species on *Meryta* or *Basselinia* in the invaded area, while *W. auropunctata* nests were associated with all but one of the 60 *Meryta* (98.3%), and 58 out of 63 *Basselinia* individuals (92.1%) (Table 3). Opening the *W. auropunctata* nests revealed the presence of several queens, a large amount of brood and several hundred to several thousand workers. We noted the presence of native Margarodidae attended by *W. auropunctata* workers on 31.4% of the sampled *Basselinia* (mean number ± SE of 15.2 ± 3.9 Margarodidae per plant). Their density was significantly higher in invaded areas compared with non-invaded areas (Wilcoxon test: W = 956.9, df = 1; P = 0.014).

DISCUSSION

The low arboreal ant species diversity recorded in the non-invaded understorey of the studied New Caledonian rain forest reinforces that found in the canopy (Jourdan & Chazeau 1999). In comparison, more than 50 ant species were recorded on only one tree by using the same technique in the Neotropical native range of *W. auropunctata* (Armbrecht *et al.* 2001, Davidson & Patrell-Kim 1996).

Most trees in inland tropical areas, including the native range of *W. auropunctata*, are occupied by 'dominant' arboreal ant species characterized by very populous colonies that defend absolute spatial territories at both the intra- and interspecific levels. Consequently, in its native range *W. auropunctata* can be excluded from arboreal resources by dominant arboreal ants (Armbrecht *et al.* 2001, Blüthgen *et al.* 2000, Tennant 1994). Also, certain ground-nesting species can compete efficiently due to their predominance in number and biomass in the ant community, their superior fighting plus recruitment abilities, or the combination of both. The fact that *W. auropunctata* monopolized all the baits and almost all tested nesting sites in the invaded areas in our study illustrates the efficiency of this species in exploiting arboreal resources, while eliminating native ants. It is equally efficient at exploiting ground-level resources (Le Breton *et al.* 2003, 2004). This competitive efficiency can be explained by the tramp ant characteristics of *W. auropunctata* (i.e., polygyny, unicoloniality, high interspecific aggressiveness) coupled with its generalist requirements for food sources and nesting sites, and by the absence of ant species capable of resisting the invader in New Caledonia. A niche opportunity is therefore available to *W. auropunctata* which also finds a favourable physical environment on the island, or the combination of a so-called escape opportunity and resource opportunity (Shea & Chesson 2002).

An escape opportunity arises when native species do not abound or are not effective in keeping out introduced species, two conditions that are true of the studied forest. We indeed noted relatively small percentages of baits and nesting sites occupied by native ants in non-invaded areas. Also, the occupation of tree baits by workers of the most frequent native species, *P. foreli*, resulted in a high discovery rate (exploitative competition), not in the active exclusion of competitors from resources (interference competition) as these workers were timid in the presence of other ant species. The same is true for other *Paratrechina* species (Davidson 1998).

A resource opportunity arises when the resources that a species needs are highly available, a situation which can be applied to the studied forest as numerous food sources and nesting sites were underexploited by

native ants before the invasion by *W. auropunctata*. The low ant species diversity noted above associated with low ant abundance and the weak exploitation of both food sources and nesting sites reflects the unbalanced characteristic (unsaturation) of the New Caledonian ant community (see also Wilson 1976). This is relevant to a more general insular pattern, since it is known that the arthropod biomass is relatively low on islands compared with mainland areas (Connor et al. 2000). Consequently, numerous resources were potentially available for *W. auropunctata* in the understorey of the studied forest. Also, colonies of this species exploit native Margarodidae much more efficiently than do native ants. This greatly increased carbohydrate supply supports a higher density of ants that in turn can consume higher quantities of other food sources such as arthropod prey. This results in a *W. auropunctata* population explosion typically much greater than the total native ant population it replaces, while saturating the invaded habitat, as has recently been pointed out for other invasive ants (Helms & Vinson 2003, O'Dowd et al. 2003).

In conclusion, the conditions necessary for a niche opportunity for *W. auropunctata* are found in this New Caledonian rain forest. In due course, once the invader has completely monopolized all available resources and saturated the area, it will not allow native ants the opportunity to re-establish. The consequences of losing these native ants, which may well interact with the diverse and endemic New Caledonian flora, are of extreme concern (Ness et al. 2004).

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LITERATURE CITED

ARMBRECHT I., JIMÉNEZ E., ALVAREZ G., ULLOA-CHACÓN P. & ARMBRECHT H. 2001. An ant mosaic in the Colombian rain forest of Chocó (Hymenoptera: Formicidae). *Sociobiology* 37: 491–509.

BLÜTHGEN N., VERHAAGH M. & GOITÍA W. 2000. Ant nests in tank bromeliads – an example of non-specific interaction. *Insectes Sociaux* 47: 313–316.

CARLQUIST S. 1974. *Island biology*. Columbia University Press, New York. 660 pp.

CONNOR E.F., COURTNEY A.C. & YODER J.M. 2000. Individuals-area relationships: the relationship between animal population density and area. *Ecology* 81: 734–748.

DAVIDSON D.W. 1998. Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. *Ecological Entomology* 23: 484–490.

DAVIDSON D.W. & PATRELL-KIM L. 1996. Tropical arboreal ants: why so abundant? Pp. 127–140 in Gibson A.C. (ed.) *Neotropical biodiversity and conservation*. Mildred E. Mathias Botanical Garden, Los Angeles.

DAVIDSON D.W., COOK S.C., SNELLING R.R. & CHUA T.H. 2003. Explaining the abundance of ants in lowland tropical rainforest canopies. *Science* 300: 969–972.

ELTON C.S. 1958. *The ecology of invasions by animals and plants*. Methuen, London. 181 pp.

[illegible] L., [illegible] T. E., SVENSSON L., [illegible] & [illegible] D. 2002. [illegible] ant invasions [illegible] archipelago. *Biological Invasions* 4: 71–88.

HELMS K.R. & VINSON S.B. 2003. Apparent facilitation of an invasive mealybug by an invasive ant. *Insectes Sociaux* 50: 403–404.

HODEL D.R. & PINTAUD J.-C. 1998. *The palms of New Caledonia*. Allen Press, Kansas. 119 pp.

HOLWAY D.A., LACH L., SUAREZ A.V., TSUTSUI N.D. & CASE T.J. 2002. The causes and consequences of ant invasions. *Annual Review of Ecology and Systematics* 33: 181–233.

HUMAN K.G. & GORDON D.M. 1999. Behavioral interactions of the invasive Argentine ant with native ant species. *Insectes Sociaux* 46: 159–163.

JAFFRÉ T. & VEILLON J.-M. 1990. Étude floristique et structurale de deux forêts denses humides sur roches ultrabasiques en Nouvelle-Calédonie. *Adansonia* 12: 243–273.

JOURDAN H. & CHAZEAU J. 1999. Les fourmis comme bio-indicateurs: l'exemple de la myrmécofaune néo-calédonienne. *Actes Colloques Insectes Sociaux* 12: 165–170.

JOURDAN H., CHAZEAU J. & BONNET DE LARBOGNE L. 2002. The recent introduction of the Neotropical tramp ant *Wasmannia auropunctata* (Roger) into Vanuatu archipelago (Southwest Pacific). *Sociobiology* 40: 483–509.

LE BRETON J., CHAZEAU J. & JOURDAN H. 2003. Immediate impacts of invasion by *Wasmannia auropunctata* (Hymenoptera: Formicidae) on native litter ant fauna in a New Caledonian rainforest. *Austral Ecology* 28: 204–209.

LE BRETON J., DELABIE J.H.C., CHAZEAU J., DEJEAN A. & JOURDAN H. 2004. Experimental evidence of large-scale unicoloniality in the tramp ant *Wasmannia auropunctata* (Roger). *Journal of Insect Behavior* 17: 263–271.

LOWE S., BROWNE M. & BOUDJELAS S. 2000. 100 of the world's worst invasive alien species. *Aliens* 12: 1–12.

MACARTHUR R.H. & WILSON E.O. 1967. *The theory of island biogeography*. Princeton University Press, Princeton. 203 pp.

MYERS N., MITTERMEIER R.A., MITTERMEIER C.G., DA FONSECA G.A.B. & KENT J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

NESS, J. H., BRONSTEIN, J. L., ANDERSEN, A. N. & HOLLAND, J. N. 2004. Ant body size predicts the dispersal distance of ant-adapted seeds: implications for small-ant invasions. *Ecology* 85: 1244–1250.

O'DOWD, D. J., GREEN, P. T. & LAKE, P. S. 2003. Invasional 'meltdown' on an oceanic island. *Ecology Letters* 6: 812–817.

SHATTUCK, S. O. 1999. *Australian ants. Their biology and identification.* CSIRO, Canberra, 226 pp.

SHEA, K. & CHESSON, P. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17: 170–176.

SIMBERLOFF, D. 1995. Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science* 49: 87–97.

TENNANT, L. E. 1994. The ecology of *Wasmannia auropunctata* in primary tropical rainforest in Costa Rica and Panama. Pp. 80–90 in Williams, D. F. (ed.). *Exotic ants.* Westview Press, Oxford.

WAY, M. J. & BOLTON, B. 1997. Competition between ants for coconut palm nesting sites. *Journal of Natural History* 31: 439–455.

WETTERER, J. K. & PORTER, S. D. 2003. The little fire ant, *Wasmannia auropunctata*: distribution, impact and control. *Sociobiology* 42: 1–41.

WILSON, E. O. 1976. Which are the most prevalent ant genera? *Studia Entomologica* 19: 187–200.