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ORIGINAL ARTICLE

Diversity of ant assemblages (Hymenoptera: Formicidae) in an urban environment in Cameroon during and after colonization of the area by *Wasmannia auropunctata*

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Abstract. Invasive species disrupt the organization and functioning of many ant communities. Little is known about ant assemblages formerly in areas invaded by the little fire ant. In this study, we surveyed the same areas and compared the ant communities there when an invasive species first colonized the areas and 10 years later, using the same methodology (quadrat and baiting). A total of 83,299 worker ants from 17 species or morphospecies, in 4 subfamilies and 10 genera were recorded in the two periods sampled. Seven ant species were found to co-occur with *W. auropunctata* while 12 species were collected in the same area 10 years later, with no *W. auropunctata* recorded in any of the traps. In the absence of *W. auropunctata*, the number and diversity of ant species increased and the ant communities were dominated by the African big-headed ant, *Pheidole megacephala*. Our findings indicate that the disappearance of *W. auropunctata* is probably related to population increases in *P. megacephala* associated with dramatic changes in landscape. Further studies at other invaded locations should be carried out in order to reveal the generality of these patterns throughout this country.

INTRODUCTION

Invasive species are recognized worldwide as one of the most important threats to biodiversity after habitat fragmentation (Rabitsch, 2011; Wittman, 2014; Orrock et al., 2015; Bertelsmeier et al., 2016). Biological invaders penetrate natural ecosystems and often reduce the diversity of native species (Human & Gordon, 1996; Hoffmann et al., 1999), affect other organisms both directly and indirectly (Meek, 2000; Jourdan et al., 2001; Laakkonen et al., 2001; Fisher et al., 2002) and severely disrupt the organization of many native communities (Mack et al., 2000; Sanders et al., 2003).

Ants are among the most problematic invasive species, threatening native biodiversity, and negatively impacting ecosystem and human health (Elton, 1958; Mack et al., 2000; Holway et al., 2002; Lach & Hooper-Bui, 2010; Rabitsch, 2011; Orrock et al., 2015). Many reports attribute the success of invasive species to behavioural and genetic changes (Hölldobler & Wilson, 1990; Passera, 1994; Holway, 1998; McGlynn, 1999; Suarez et al., 1999; Tsutsui et al., 2000; Tsutsui & Suarez, 2003), release from natural enemies and new opportunities for resources in their introduced ranges (Clark et al., 1982; Settle & Wilson, 1990; Ulloa Chacón, 1990; Mack et al., 2000; Shea & Chesson, 2002; Le Breton et al., 2005). According to Holway et al. (2002), six ants are recognized as the most widespread and damaging invasive species: *Anoplopepis gracilipes* (yellow crazy ant), *Linepithelma humile* (Argentine ant), *Pheidole megacephala* (African big-headed ant), *Solenopsis invicta* (red imported fire ant), *Solenopsis geminata* (tropical fire ant) and *Wasmannia auropunctata* (little fire ant).

Wasmannia auropunctata Roger, 1893 is one of the most harmful invasive species in the world (Wetterer & Porter, 2003). Native to Central and South America, *W. auropunctata* has been introduced throughout the West Indies, Australia, Israel, Italy, Pacific islands groups and West Africa (Wetterer, 2013). In Cameroon, *W. auropunctata* was first reported in cocoa plantations along the Kribi-Ebolowa road (de Miré, 1969). Since then, it has successfully spread into southern and eastern Cameroon (Tindo et al., 2012), where it has severely reduced the abundance and richness of native ant species (Mbenoun et al., 2017).

The invasive success of exotic species can vary substantially over time from population explosions to population

Fig. 1. Map showing the location of the study site in 2007 (A) and in 2017 (B).

collapses or dramatic population declines. These phenomena have been reported for a wide range of invasive species, including snails and crayfish (Simberloof & Gibbons, 2004; Sandström et al., 2014). With regard to invasive ants, Morrison (2002) reports that red fire ants (*Solenopsis invicta*) decreased in Texas over 12 years. Similarly, populations of Argentine ant (*Linepithelma humile*) have decreased at 40% of the sites surveyed, with a mean survival time of 14 years (Cooling et al., 2012). More recently, yellow crazy ant (*Anoplolepis gracilipes*) populations have declined or disappeared in Australia without human intervention (Cooling & Hoffmann, 2015).

Although invasive ants may initially exterminate native ants, ant communities have recovered in environments previously invaded by *Solenopsis invicta* (Morrison, 2002; Calixto et al., 2007), *Pheidole megacephala* (Torres & Snelling, 1997) and *Linepithema humile* (Wetterer et al., 2006; Cooling et al., 2012). However, with regard to *W. auropunctata*, little is known about the ant assemblages in areas several years after they were colonized by this ant. In this study, we hypothesized that native ant communities in an area may recover some time after being colonized by an invasive species.

MATERIAL AND METHODS

Study area

This study was first carried out in 2007 and repeated in 2017 in Biyem-Assi (3°51′83″N, 11°27′76″E) (Fig. 1), an urban district of Yaoundé (political capital of Cameroon). The vegetation in Yaoundé was semi-deciduous forest, but currently is a mixture of relic forest on summits of hills and garden crops (urban agriculture) along river and inland valleys. The wet season is from March to June, followed by a short dry season from July to the end of August, a short wet season from September to mid-November and a long dry season from mid-November to February. Average annual rainfall is about 1,500 mm. The mean annual relative humidity is 79.5%. Mean air temperature ranges from 19.2 to 28.6°C. *Wasmannia auropunctata* was first detected at this location in 1998 during a preliminary survey of its distribution in Cameroon (Tindo et al., 2012). Since the first survey in 2007, the landscape of this location has dramatically changed and is now characterized by build-up areas, fewer green spaces and less vegetation

Sampling methods

The methodology used by Mbenoun et al. (2017) for sampling in 2017 was replicated as closely as possible at the same plots where *W. auropunctata* were previously found. Eight transects were established extending in four directions (East, West, South and North) from areas previously colonized by the invasive ant and those not colonized. At each previously colonized area, starting from randomly selected points and going in each of the four cardinal directions, two parallel lines (150 m long and 2 m wide) spaced 10 m apart were established. Sampling points were established every 10 m along the transect lines giving a total of 30 samples (15 samples × 2 transects × 1 direction of invasion). These transects were surveyed once a month over a period of 12 months. Ant species richness and occurrence were monitored at the same areas previously sampled in 2007 that were colonized by *W. auropunctata*, using ground baiting and quadrat sampling (Bestelmeyer et al., 2000).

Ground baiting

Baits consisted of 20 cm × 20 cm square plastic trays containing a mixture of honey 30%, tuna 50% and soya oil 20%. Fifteen bait stations were placed along each transect line 10 m apart. Ants were checked on the bait after 30 min to 60 min and collected using forceps and a pooter. Samples were stored in vials containing 70% ethanol and transferred to the laboratory for counting and identification.

Quadrat sampling

Fifteen 1 m^2 quadrats were established along the second transect line (10 m apart). Within each, we actively searched for ants in rotten logs and stumps, dead and alive branches and twigs, low vegetation and under stones for 15 min. A total of 180 quadrats were sampled in each cardinal direction during the sampling period. Ants found were collected using forceps and a pooter, stored in vials containing 70% ethanol and transferred to the laboratory for counting and identification.

Specimen processing

In the laboratory of Zoology at the University of Yaoundé I, ants were identified to species level (or to morpho-species) using keys from Hölldobler & Wilson (1990) and Bolton (1994) for genera, and the web site "Ants of sub-Saharan African" (Taylor,

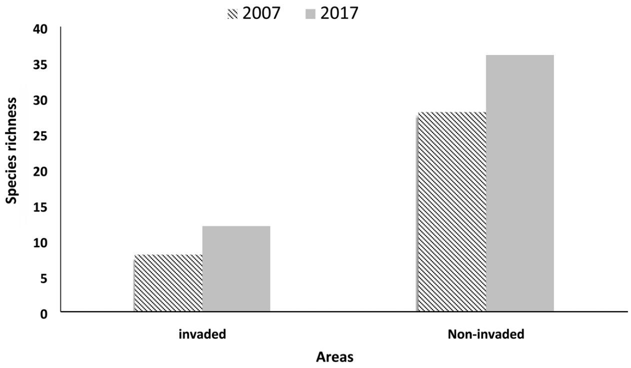

Fig. 2. Species richness recorded in areas invaded and not invaded by *W. auropunctata* in 2007 and 2017.

2011) for species. Ant specimens were mounted on card board triangles and then kept as a reference collection in the laboratory.

Statistical analysis

For analysis, data were entered on a matrix in the form of presence-absence data, a fundamental unit of study in community ecology and biogeography. The percentage of occurrence was used to estimate the relative abundance of all species at each site. To estimate the species richness in the two periods sampled, Margalef richness index (R1) and Menhinick index (R2) were calculated using the following formulae:

$$R1 = \frac{S-1}{\ln(N)} \quad \text{and} \quad R2 = \frac{S}{\sqrt{N}}$$

where S is the number of species and N is the total number of individuals.

To evaluate the diversity in the two periods sampled, Shannon-Weaver diversity index (H´) and Pielou's equitative index (J´) were used while evenness was analysed using Simpson dominance index (D).

$$H' = -\sum_{i=1}^{S^*} \left(p_i * \log_2 p_i\right)$$

where p is the proportion of individuals in the i^{th} order.

$$J' = \frac{H'}{H_{max}} = \frac{H'}{\ln(S)}$$

where $H_{max} = Log_2(S)$.

$$D = \sum_{i=1}^{S} \frac{n_i(n_i-1)}{N(N-1)}$$

where n_i = the number of individuals of species "i" and N = the total number of individuals.

Then these parameters for 2007 and 2017 were compared using the parametric Student's *t* test when the data were normally distributed. All statistical tests were carried out using SPSS software version 16.0 for Windows.

RESULTS

Structure of the ant assemblages

A total of 83,299 worker ants belonging to 17 species or morphospecies in 4 subfamilies and 10 genera were recorded in the two periods sampled (Table 1). Myrmicinae was the most species-rich subfamily with 11 species, followed by Formicinae (3 species) and Dolichoderinae (2 species). The most species-rich genus was *Pheidole* (4 species) followed by *Monomorium* (3 species) and *Camponotus* and *Tapinoma* with 2 species each.

Ant composition in the two periods

In 2007, eight species of ants were collected in invaded areas (Fig. 2). *Wasmannia auropunctata* was the most frequent species (140 occurrences; 89.17%) (Fig. 3A) and co-occurred with seven species: *P. megacephala* (10 occurrences; 6.37%), *Monomorium bicolor* (2 occurrences; 1.27%) and *Myrmicaria opaciventris, Tapinoma carininotum, Paratrechina longicornis, Tetramorium simillimum, Solenopsis geminata* (1 occurrence, 0.64% each). Ten years later, 12 ant species were collected with no *W. auorpunctata* recorded in any of the traps. The most common species was *P. megacephala* (74.74%) (Fig. 3B), followed

Table 1. List of the species of ants occurring in the area studied when (2007) and after (2017) it had been colonized by *W. auropunctata.* AF – Africa, AF* – Africa and endemic in Cameroon, CS – Central America, SA – South America.

Subfamilies / species	Native range	2007	2017
Dolichoderinae			
Tapinoma carininotum Weber, 1943	AF	5	14
Tapinoma sp.	AF	0	4
Formicinae	AF		
Camponotus (*Tanaemyrmex*) *maculatus* (Fabricius, 1782)	AF	0	8
Camponotus (*Tanaemyrmex*) *acvapimensis* Mayr, 1862	AF	0	14
Paratrechina longicornis (Latreille, 1802)	AF	5	0
Myrmicinae	AF		
Monomorium guineense (Bernard, 1953)	AF	0	10
Monomorium bicolor Emery, 1877	AF	8	6
Myrmicaria opaciventris Emery, 1893	AF	9	2542
Pheidole megacephala (Fabricius, 1793)	AF	24	45006
Pheidole minima Mayr, 1901	AF*	0	13
Pheidole tenuinodis Mayr, 1901	AF	0	4
Pheidole sp.4	AF	0	4
Solenopsis geminata (Fabricius, 1804)	CS, SA	5	0
Tetramorium simillimum (Smith, 1851)	AF	5	0
Wasmannia auropunctata Roger 1863	CS, SA	35609	0
Ponerinae			
Hypoponera cognata (Santschi, 1912)	AF	0	4

by *Myrmicaria opaciventris* (10.77%) and *Camponotus acvapimensis* (3.93%).

In the non-invaded areas, 28 and 36 species of ants were collected in 2007 and 2017, respectively (Table 2). The most common species were *Pheidole megacephala,* (35.63% and 62.57%) followed by *Solenopsis geminata* (20.61% and 3.55%) and *Paratrechina longicornis* (10.71% and 1.89%) in 2007 and 2017, respectively.

Species turnover, diversity and evenness

Three ant species (*Paratrechina longicornis, Solenopsis geminata* and *Tetramorium simillimum*) that were present in initially invaded areas were absent in 2017. In contrast, eight species (*Tapinoma* sp., *Camponotus acvapimensis, Camponotus maculatus, Monomorium guineense, Pheidole tenuinodis, P. minima, Pheidole* sp.4 and *Hypoponera cognata*) that were absent in initially invaded areas were present in 2017. The occurrence of two species *P. mega-*

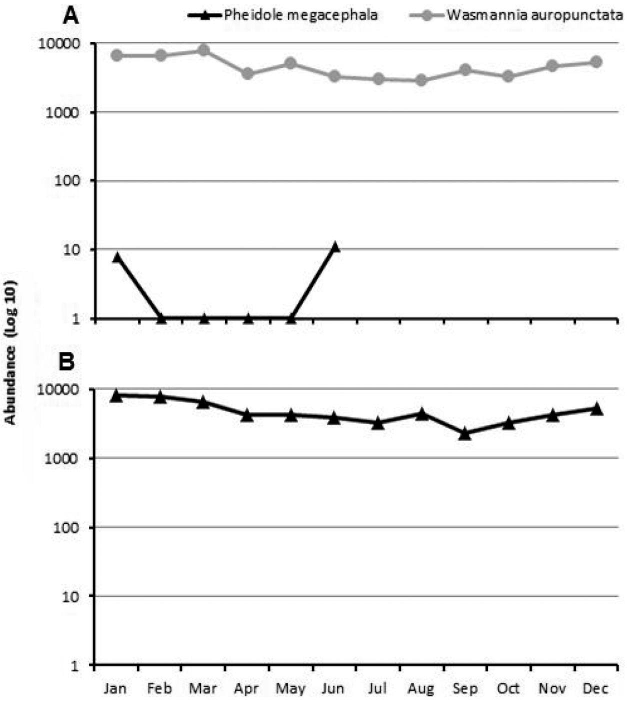

Fig. 3. Abundance (Log$_{10}$) of *Pheidole megacephala* and *Wasmannia auropunctata* at sites when *W. auropunctata* was present (2007) (A) and absent (2017) (B).

Table 2. Relative frequency of the different species of ants in areas invaded and not invaded by *W. auropunctata* in 2007 and 2017.

Subfamilies / species	2007		2017	
	Invaded	Not-invaded	Invaded	Not-invaded
Aenictinae				
Aenictus decolor (Mayr, 1879)	–	0.43	–	0.07
Cerapachyinae				
Lioponera coxalis (Arnold, 1929)	–	0.01	–	–
Dolichoderinae				
Tapinoma carininotum Weber, 1943	0.64	11.09	2.9	2.08
Tapinoma sp.	–	–	0.21	0.01
Technomyrmex albipes (Smith, 1861)	–	0.06	–	0.01
Dorylinae				
Dorylus (*Anomma*) *nigricans* Illiger, 1802	–	0.26	–	0.05
Dorylus (*Dorylus*) sp.	–	0.56	–	0.09
Formicinae				
Camponotus (*Myrmotrema*) sp.1	–	0.25	–	0.05
Camponotus (*Myrmotrema*) sp.2	–	0.10	–	0.02
Camponotus (*Tanaemyrmex*) *maculatus* (Fabricius, 1782)	–	–	0.83	0.01
Camponotus (*Tanaemyrmex*) *acvapimensis* Mayr, 1862	–	–	3.93	0.05
Lepisiota sp.1	–	0.07	–	0.01
Lepisiota sp.2	–	0.11	–	0.09
Lepisiota sp.3	–	–	–	0.21
Paratrechina longicornis (Latreille, 1802)	0.64	10.71	–	1.89
Myrmicinae				
Monomorium pharaonis (Linnaeus, 1758)	–	6.36	–	1.74
Monomorium guineense (Bernard, 1953)	–	0.14	2.07	0.04
Monomorium sp.3	–	–	–	0.06
Monomorium bicolor Emery, 1877	1.27	2.06	1.24	0.78
Myrmicaria opaciventris Emery, 1893	1.27	4.50	10.77	3.57
Pheidole sp.2	–	0.08	–	0.07
Pheidole megacephala (Fabricius, 1793)	6.37	35.63	74.74	62.57
Pheidole speculifera Emery, 1877	–	5.12	–	0.86
Pheidole minima Mayr, 1901	–	–	2.68	0.25
Pheidole tenuinodis Mayr, 1901	–	–	0.21	0.01
Pheidole sp.4	–	–	0.21	0.06
Solenopsis geminata (Fabricius, 1804)	0.64	20.61	–	3.55
Tetramorium simillimum (Smith, 1851)	0.64	0.22	–	0.11
Tetramorium sp.2	–	0.07	–	0.03
Tetramorium aculeatum (Mayr, 1866)	–	0.19	–	0.03
Tetramorium longicorne Forel, 1907	–	0.08	–	0.17
Tetramorium coloreum Mayr, 1901	–	0.05	–	0.01
Wasmannia auropunctata Roger 1863	89.17	–	–	
Ponerinae				
Odontomachus troglodytes Santschi, 1914	–	0.38	–	0.06
Brachyponera sennaarensis (Mayr, 1862)	–	0.67	–	0.11
Paltothyreus tarsatus (Fabricius, 1798)	–	0.17	–	0.03
Hypoponera cognata (Santschi, 1912)	–	–	0.21	–
Pseudomyrmecinae				
Tetraponera ledouxi Terron, 1969	–	–	–	0.01

Table 3. Species richness, diversity, equitability and evenness in areas invaded by *W. auropunctata* in 2007 and in 2017 when this species had disappeared.

Parameters	Invaded area		Student's *t* test		
	2007	2017	*t*	*df*	*P*
Species richness (S)	8	12			
Individuals (N)	35670	47629			
Margalef (R1)	0.66	1.02			
Menhinick (R2)	0.04	0.05			
Simpsom (D)	0.9983	0.8563	25.32	11	>0.05 ns
Shannon (H´)	0.007994	0.3495	72.04	11	<0.001***
Pielou (J´)	0.003638	0.1363	59.34	11	<0.001***

ns – non-significant; ***P < 0.001 – highly significant difference at 5% confidence interval.

cephala and *M. opaciventris* was significantly greater in 2017.

Species richness and number of individuals were higher in 2017 (N = 47629; S = 12) than in 2007 (N = 35670; S = 8). Despite this difference in species richness, Margalef and Menhinick richness estimators indicate that these values were very low and tended towards zero. The ant communities were more diverse and heterogeneous in 2017 (H´ = 0.349; J´ = 0.136) than in 2007 (H´ = 0.007; J´ = 0.003), with significant differences in both the Shannon-Weaver (Parametric t test: $t = 72.04$; $P < 0.001$) and Pielou indices (Parametric t test: $t = 59.34$; $P < 0.001$) (Table 3). In 2007, the ant communities were almost mono-specific and dominated by *W. auropunctata* (D = 0.99), whereas *P. megacephala* dominated ant communities in 2017 (D = 0.85). There was no difference in species evenness in the two years sampled (Parametric t test: $t = 25.32$; $P > 0.05$).

DISCUSSION

Our results highlight differences in the structure of native ant assemblages in the presence and absence of *W. auropunctata*. Indeed, in areas colonized by this ant, native ant species richness was very low, whereas ten years later when *W. auropunctata* was no longer present it was much higher. In areas invaded by this species not only have a reduced species richness but also disassembled communities (Mack et al., 2000; Sanders et al., 2003). However, the abundance of many invasive species may vary substantially over time and recovery or resurgence of native ant communities is possible after they decline in abundance or disappear (Torres & Snelling, 1997; Morrison, 2002; Wetterer et al., 2006; Calixto et al., 2007).

The present study documented the disappearance of *W. auropunctata* in an urban district in Cameroon. A previous ecological study in the same area indicated the contraction of population along different invasion fronts during a 6-year period (Tindo et al., 2012). Although population collapses or substantial declines are recorded for other invasive species of ants, such as: *Linepithema humile* (Argentine ant) (Wetterer et al., 2006), *Anoplolepis gracilipes* (yellow crazy ant) (Abbott & Green, 2007), *Pheidole megacephala* (big-headed ant) (Torres & Snelling, 1997; Wetterer et al., 2006), *Solenopsis geminata* (tropical fire ant) (Wilson, 2005) and *Solenopsis invicta* (imported red fire ant) (Morrison, 2002), the mechanisms driving the declines are still unclear. Several hypotheses have been suggested, such as, infection by local pathogens or attack by parasites, fire, pesticides, migration, over exploitation of resources, climate, changes in the food availability, vegetation and population bottlenecks in introduced ranges (Haines & Haines, 1978; Russell-Smith et al., 1997; Wetterer et al., 1998, 2006; Mikheyev & Mueller, 2007; Lester & Gruber, 2016). Other biotic factors, like competitive exclusion of *W. auropunctata* by dominant native ants might account for the disappearance of *W. auropunctata* in both previously invaded and surrounding areas. The competitive exclusion principle predicts that interspecific competition results in the elimination or extinction of one of two species that occur together without niche differentiation (Webb et al., 2002; Bøhn et al., 2008). In accordance with our previous findings (Mbenoun et al., 2017) and other studies (Tennant, 1994; Le Breton et al., 2003), some dominant species, particularly ants of the genus *Pheidole*, can co-occur in the same plots with *W. auropunctata* and may keep its population densities low. In addition, *P. megacephala* is numerically the dominant species in ant communities in its native range (Dejean et al., 2008; Mbenoun et al., 2017). In contrast, *W. auropunctata* never dominates ant communities in its native range and several species of *Pheidole* are important competitors and may significantly reduce its population density (Levings & Franks, 1982; Tennant, 1994).

Although *P. megacephala* dominates native communities of ants and exhibits unicolonial social structure even in its native range, which is key factor determining its ecological dominance (Fournier et al., 2012), this species is able to coexist with other native ants with similar foraging and dietary requirements. Dejean et al. (2008) point out that only colonies of *Solenopsis geminata, Dorymyrmex pyramicus* and *Dorichoderus bispinosus* resisted raids by *P. megacephala* in its introduced range, whereas 11 of 12 species in its native range resisted raids by the workers of *P. megacephala*.

In conclusion, this study revealed that the structure of ant assemblages change over time. It highlights that native ant communities can be transiently invaded by *W. auropunctata* and might recover over time. The population increase in African big-headed ant *P. megacephala* and dramatic changes in the landscape between 2007 and 2017 might account for the disappearance of *W. auropunctata* in the area studied. Therefore, further studies at other invaded sites should be carried out in order to reveal the consistency of these results and understand the mechanisms that cause population declines or local extinctions of the little fire ant.

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