Interaction and resource exploitations between invasive and native ants in cocoa and surrounding farmlands in southern Cameroon rainforest

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Abstract
Here, we studied the interaction and assessed the exploitation of feeding and nesting resources by exotic versus local ants in farmlands in 2010 and 2021 in southern Cameroon. We considered invaded and non-plots by the invasive ant Wasmannia auropunctata and randomly selected and checked plant species for the presence of native ants and associated resources like Extrafloral Nectaries (EFN), Honeydew Producing Hemipterans (HPH) and Shelters (SH). Twenty-five out of 31 plants species were checked bore distributed as follow: 56% of EFN, 52% of HPH and 48% of SH. In non-invaded plots, eight native ant species were found exploiting 48% of EFN and SH and attended eight morpho-species of hemipterans while W. auropunctata was found on 100% of resources and attended 12 morpho-species of hemipterans with Stictococcus sjostedti (Stictococcidae) being the most abundant in invaded plot. These findings support “niche opportunity hypothesis” in W. auropunctata and demonstrate its ability to dominate resources and to attend more hemipterans unlike native ants.

Keywords: Resource, W. auropunctata, resource, native ants, Cameroon

Introduction
Ants are highly diverse and distributed in all continents except Antarctica (Hölldobler & Wilson, 1990) [16]. Owing to their widespread success, ants are considered as one of the most devastating groups of invaders among social insects (Chapman & Bourke, 2001, O'Dowd et al., 2003, Vinson, 1999, Williams & Vail, 1993) [5, 38, 47, 54]. Invasive ants form a small (at least 150 species) within tramp species which are introduced into new environments by human (McGlynn, 1999) [32]. Many features are found in invasive ants such as mass-recruitment, absence of intraspecific aggression, unicoloniality, high interspecific aggression, the bidding of nest, and opportunist for food and nest location (Passera, 1994) [39]. In addition to the tendency for introduced populations to be unicolonial, invasive ants share other characteristics that increase their ability to invade new habitats, such as omnivory, and phylogenetic and morphological diversity (Holway et al., 2002a) [17]. All these traits are involved in the decline of invertebrates and vertebrates in areas where invasive ants has been accidently introduced (Allen et al., 1995, Feare, 1999, Jourdan, 1999, Laakkonen et al., 2001, Le Breton et al., 2003, Meek, 2000, Mikassa et al., 2008, Vonshak et al., 2009, Walker, 2006, Wetterer & Porter, 2003, Wetterer et al., 1999) [2, 13, 22, 23, 24, 33, 34, 48, 49, 52, 53].

The little fire ant Wasmannia auropunctata Roger is native to Central and South America. This invader has been introduced into various island groups in the Caribbean and Pacific Oceans, Australia, Florida and Israel (Vonshak et al., 2009, Wetterer & Porter, 2003) [48, 52]. Wasmannia. auropunctata has also been found in tropical green houses in Great Britain and Canada (Ayre, 1977) [3]. In Africa, it was first reported in Gabon (Ndoutoume & Mikassa, 2007, Santschi, 1914, Walker, 2006, Walsh et al., 2004, Wetterer & Porter, 2003, Wetterer et al., 1999, Mikassa et al., 2008) [37, 42, 49, 50, 52, 53, 34], where it has invaded both human disturbed and natural forest environments, and later in Cameroon (Tindo et al, 2012) [46]. The first records of W. auropunctata infestation in Cameroon come from 1962 in the Cameroonians coastal region, where cacao (Theobroma cacao) growers purposely transported W. auropunctata colonies from plantation to plantation as a biological control agent of certain insects pest, particularly Miridae (Hemiptera) (de Miré, 1969) [8].
Wasmannia auropunctata is one of the worst exotic pest ants (Lowe et al., 2000) [27]. This invasive species is responsible for reducing ant and other invertebrate abundance and species diversity on oceanic islands (Abedrabbo, 1994, Clark et al., 1982, Jourdan, 1997, Lubin, 1984, Wetterer & Porter, 2003, Wetterer et al., 1999) [1, 22, 28, 52, 53]. Continental lands are less susceptible to bio-invasion due to their high species richness (Rejmánek, 1996) [41] compared to islands. It has been hypothesized that a community with many species is unlikely to have any vacant niches that cannot be defended successfully from an immigrant (Elton, 1958) [12]. Here, we examined the ability of W. auropunctata and native ants to exploit feeding and nesting resources in cocoa and surrounding farmlands in southern Cameroon. We also evaluated the interaction between exotic and local ants, and population densities of hemipterans attended by each ant groups.

Materials and Methods

Investigations were carried out in 2010 and 2021 in southern Cameroon rainforest in three locations: Nko’ondo (2°31’82”N; 10°53’55”E), Ngomedzap (3°14’51”N; 11°14’43”E), and Akonetye (2°31’89”N; 10°55’14”E). Wasmannia auropunctata was found in Nko’ondo and Akonetye during preliminary investigation carried out on spatial distribution of this ant (Tindo et al., 2012) [46]. In these sites as in other invaded plots in Cameroon, W. auropunctata has mainly occupied disturbed habitats around houses (e.g cassava field, cocoa farms, etc) and along roads. Ngomedzap is one site no yet invaded by W. auropunctata and use as control site. The southern Cameroon experiences an equatorial climate of the Guinea subtype characterized by four distinct seasons: two wet seasons and two dry seasons. Rainfall is high especially along the coast. Rainfall averages 1500-2000 mm per year and the mean annual temperature is about 25 °C. To assess exploitation of feeding and nesting resources, we monitored species richness and abundance in ground and arboreal stratum in invaded and non-invaded plots by W. auropunctata.

At ground level, we assessed the exploitation of feeding resources by baiting (mixture of sardine in conserve and honey). At each location, 3 transects (90 m long and 5 m apart) were delimited. Along of 45 m delimited in each area, we placed ten baits on the ground on a square plastic (10 x 10 cm). Four sampling events were conducted in each location. Baits were deposited between 8h00 and 10h00, revisited after two hours and ant identity and density were evaluated either in situ (when possible) or collected and preserved in vials containing 70% alcohol for further identification in the laboratory.

At the arboreal stratum, we randomly selected and checked plant species for the presence of ants and associated resources like extrafloral nectaries (EFN), honeydew producing hemipterans (HPH) and shelters (SH). Sampling was conducted on small plants (maximum height 2 meters). For each host plant, we collected ant species directly from the EFN. HPH and SH resources using forceps and an aspirator. Density of hemipteran species attended by W. auropunctata and local ants in each host plant was estimated. Plants that could not be identified on-site were collected, hard-pressed dried and identified at the Cameroon National Herbarium. A Student t-test was performed to compare means between native ants and W. auropunctata populations and density of homopteran was compared using Chi-square (SPP version 12.0 software).

Results

Structure ant assemblages

A total of 28 species, belonging to 21 genera and 8 subfamilies were collected on the baits and on the sampled plants. With 14 species and 9 genera, the Myrmicinidae was the most speciose and abundant subfamily, followed by the Formicinae (6 species and 4 genera). The most species-rich genus was Tetramorium (4 species).

At ground stratum

Sixteen ant species were collected in 240 baits placed in both invaded and non-invaded plots. In non-invaded plots, 15 ant species were caught namely: Technomyrmex parandrei, Tapinoma carinatum, Camponotus bradus, Camponotus sp.2, Camponotus sp.3, Paratrechina sp.1, Cremaefager (atopoyne) sp., Cremaefager (sphaerocrema) striatula, Myrmicaria opaciventris, Pheidole tenuinodis, Pheidole speculifera, Tetramorium aculeatum, Odontomachus troglodytes, Pachycondyla tarsata Polyrachis militaris, Tetramorium aculeatum and M. opaciventris were most abundant. Indeed, these two species accounted for 35 and 23% of total species collected respectively (Fig. 1). In contrast, W. auropunctata monopolized 100% of baits in invaded plots. No other species of ant was found on baits or in a radius of 50 cm between them. Statistical different was found between the two plots (Student t-test: t = 17.75; df = 35; p<0.001).

At the arboreal stratum

Thirty-one plant species belonging to 23 families were identified (Table 1). Twenty-five out of 31 plants species checked bore distributed as follow: 56% (14/25) of extrafloral nectaries, 52% (13/25) of honeydew producing hemipterans and 48% (12/25) of shelters. Of the six plants remaining, we observed foragers. W. auropunctata was the only ant species detected in 100% of plants in invaded plots while only 38.71% of the plants were occupied by local ants in non-invaded plots. Statistical difference was found between the number of ant species present on each plant species in the two areas (Student t-test: t = 14.23; df = 35; p<0.001).

Feeding resource

In non-invaded plots, six out of 14 plants (42.85%) with extrafloral nectaries (Mangifera indica L. (Anacardiaceae) Dacryodes edulis G (Burseraceae) Costus afer ker Gawl. (Costaceae) Costus littoralis K.Schum. (Costaceae) Persea americana Mill. (Lauraceae) and Psidium guajava L. (Myrtaceae)) were occupied by local ant. In contrast, all these plants were completely occupied by W. auropunctata in invaded area.

We recorded 17 morpho-species of hemipterans belonging to 6 families on 13 plant species. The most speciose family was Aphididae (6 species), followed by Stictococcidae (4 species), Psilliidae (3 species), Coccidae (2 species), Miridae...
and Membracidae with one species each. In non-invaded plot, eight morpho-species of hemipterans were found with six native ants: *Technomyrmex albipes*, *Crematogaster (sphaerocrema) striatula*, *Pheidole tenuinodis*, *Tetramorium aculeatum*, *Crematogaster (sphaerocrema) zavattarii*. In invaded plots, *W. auropunctata* attended 12 morpho-species of hemipterans. Amongst them, *W. auropunctata* was mostly found with high population of *Stictococcus sjoestedti* (Stictococcidae) on cacao trees (*Theobroma cacao*) (Fig. 3).

**Nesting resource**

Five plant species out of twelve (42%) sheltered ant nests belonging to eight local ant species in invaded plots (Fig. 2). These nests were found in large numbers on cocoa plants (*Theobroma cacao*) under the leaves (*Tetramorium aculeatum* Mayr and *Oecophylla longinoda* Latreille); in the dead branches (*Catalaicus kohli* Mayr, *Crematogaster (Sphaeroercrema) striatula* Emery and *Crematogaster (Sphaeroercrema) zavattarii* Menozzi; in dried cherelles (*Polyrachis decendentata* Andre and *Axinidus* sp.) and in cavities between trunk (*Pheidole tenuinodis* Mayr). The most common ant species in shelters were *Te. aculeatum* (35%) followed by *Ph. Tenuinodis* (28.3%). In invaded plots, *W. auropunctata* was found in 100% of nesting resources. Queens and brood were found in cavities under the bark (*Mangifera indica* L., *Dacryodes edulis* G., *Theobroma cacao* L., *Psidium guajava* L.), at the interstices of the branches forming the hanging soil (*Elaeis guineensis* Jacq., *Dacryodes edulis* G., *Theobroma cacao* L.), at the armpits of leaves (*Anthcleista schwefinfurthii* Gog., *Dalbergia saxatilis* Hook. *Costus littoralis* K. Schum., *Costus afer* Ker Gawl) and at the base of the trunk (*Phyllostachys* sp., *Musa* sp.).

**Discussion**

Although Cameroon had high ant species richness (Deblauwe & Dekoninck, 2007, Watt et al., 2002) [8, 51], the presence of invasive ant *W. auropunctata* means that opportunities exist but seem to be localized only in disturbed area (de Miré, 1969, Wetterer & Porter, 2003) [8, 52] and absent in natural area such as primary forest (Tindo et al., 2012). *W. auropunctata* is disturbance specialist (Majer & Delabie, 1999) [10], and when ant species are organized in structured ant communities (no disturbance), potential pest ants are regulated by competition or predation and cannot reach high population densities.

Our results show that compared to the local ants, *W. auropunctata* completely monopolizes resources at the ground level and lower arboreal level as well. Of the Formicidae, a relationship often exists between the ability of a species to discover food and its ability to dominate resources behaviorally or numerically (Banks & Williams, 1989, Fellers, 1987, Johnson, 1981, Morrison, 1996, Nagamitsu & Inoue, 1997, Wilson, 1971) [4, 15, 19, 35, 36, 56]. However, compared to native ants, invasive ants may excel at both resource discovery and resource dominance, effectively breaking the trade-off (Davidson, 1998, Feener, 2000) [7, 14]. For example, in New Caledonian dry forest, when *W. auropunctata* is present it demonstrates a fast and durable conquest of baits while the cohabitation of various species and their succession on the baits were observed in the area where this invasive is absent (Delsinne et al., 2001) [11], suggesting the ability of *W. auropunctata* to break down the classical trade-off between resource discovering and resource monopolization expressed by most invasive ants species. In addition, the success of invasive species has mainly been attributed to unicoloniality and niche opportunities, which apparently occurred in the introduction area (Hodway et al., 2002b, Shea & Chesson, 2002) [18, 44]. The fact to be unicolonial in introduction area enables *W. auropunctata* to form expansive and polygynous supercolonies that lack distinct behavioral boundaries among physically separate nests. Indeed, large colony size enhances exploitation ability because it simultaneously maintain large forces of scouts (i.e., workers actively searching for food) and recruits (i.e., workers in the nest available to help exploit rich food discoveries) (Johnson et al., 1987) [20]. A niche opportunity is the potential provided by a given community for alien organisms to have a positive rate of increase from low density. This might occur because of “a resource opportunity”, “an escape opportunity” or a combination of both (Shea & Chesson, 2002) [44]. “A resource opportunity” is defined as a high availability of resources on which a potential invader depends. Disturbance is commonly assumed to release resources and provide opportunities for invaders. Indeed, Humans activities through culture and plantation increase the disruption of native communities in southern Cameroon. Consequently, populations of dominant arboreal ants such as *Crematogaster africana* and *Oecophylla longinoda* are regularly disturbed offering resource availability for opportunists like *W. auropunctata*. “An escape opportunities” arise when natural enemies, such as diseases, predators and parasites, are in low abundance or are less effective against new species (Settle & Wilson, 1990) [43]. This situation is generally true for islands where Le Breton et al., (2007) [24] showed unadapted behaviour of native, dominant ant species against *W. auropunctata* in New Caledonian. In its native range, *W. auropunctata* is regarded as non-dominant in undisturbed areas such as the rainforest and several ant species, particularly of the genus *Pheidole*, compete successfully against *W. auropunctata* and may help keep its population densities low (Levings & Franks, 1982, Tennant, 1994) [26, 45]. In central Africa, a native dominant ant *Pheidole megacephala* can compete with territorially dominant arboreal ants in the low canopies of cocoa tree plantations (Dejean et al., 2005) [10]. Unfortunately, this ant species was no found during sampling in rural area. Tindo et al. (2012) [40] showed an overall reduction in the surface area colonized by *W. auropunctata* and suggested to investigate the causes of this reduction, particularly the response of local ant species: *Pheidole megacephala* and *Myrmecaria opaciventris*. Recent studies on impact and competitive interactions demonstrated that *P. megacephala* is the most common ant species in transition and non-invaded areas by *W. auropunctata* in urban ecosystem of Yaoundé, Cameroon. It also efficiently defends resources against *W. auropunctata* in the laboratory and in the field. Therefore, this local ant may reduce population of *W. auropunctata* and could probably be responsible for the reduction of the surface colonized by invader.
### Table 1: Family and plant species, resource and number of ant species encountered by plant species in invaded and non-invaded by *W. auropunctata* (N = 31 plant species recorded). EFN= extrafloral nectaries; HPH = honeydew producing hemipterans; SH = shelters

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Resource</th>
<th>Ant species collected in each plant species</th>
</tr>
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<tbody>
<tr>
<td></td>
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<td>Invaded area</td>
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<tr>
<td>Anacardiaceae</td>
<td>Mangifera indica L.</td>
<td>EFN, SH</td>
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<tr>
<td>Arecaceae</td>
<td>Elaeis guineensis Jacq.</td>
<td>SH</td>
<td>1</td>
</tr>
<tr>
<td>Asteraceae</td>
<td>Chromolaena odorata L.</td>
<td>HPH</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Elephantopus mollis L.</td>
<td>HPH</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Vernonia bamudae C.</td>
<td>EFN</td>
<td></td>
</tr>
<tr>
<td>Bignomaceae</td>
<td>Newbouldia laevis N. Beauv.</td>
<td>EFN, HPH</td>
<td>1</td>
</tr>
<tr>
<td>Burseraceae</td>
<td>Daecryodes edulis G.</td>
<td>EFN, SH</td>
<td>1</td>
</tr>
<tr>
<td>Cecropiaceae</td>
<td>Musanga cecropioides R. Br.</td>
<td>HPH</td>
<td></td>
</tr>
<tr>
<td>Costaceae</td>
<td>Costus afer ker Gawl.</td>
<td>EFN, SH, HPH</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Costus littoralis K. Schum.</td>
<td>EFN, SH, HPH</td>
<td>1</td>
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<tr>
<td>Dioscoreaceae</td>
<td>Dioscorea bulbifera L.</td>
<td>EFN</td>
<td>1</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td>Alchornea cordifolia Schmach.</td>
<td>HPH</td>
<td>1</td>
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<td></td>
<td>Bridelia macrantha Hochst.</td>
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<td></td>
<td>Macaranga spinosa Müll. Arg</td>
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<tr>
<td>Fabaceae</td>
<td>Dalbergia saxatilis Hook.</td>
<td>SH</td>
<td>1</td>
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<tr>
<td>Lamiaceae</td>
<td>Solenostome latifolia</td>
<td>EFN</td>
<td>1</td>
</tr>
<tr>
<td>Lauraceae</td>
<td>Persea americana Mill.</td>
<td>EFN, SH</td>
<td>1</td>
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<tr>
<td>Loganiaceae</td>
<td>Anthocleista schweinfurthii Gilg.</td>
<td>EFN, SH, HPH</td>
<td>1</td>
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<tr>
<td>Malvaceae</td>
<td>Sida acuta Burm.</td>
<td>EFN</td>
<td>1</td>
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<tr>
<td></td>
<td>Theobroma cacao L.</td>
<td>SH, HPH</td>
<td>1</td>
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<td></td>
<td>Triumfetta cordifolia A Rich.</td>
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<tr>
<td>Mimosaceae</td>
<td>Albizia zygia Gum.</td>
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<td>1</td>
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<tr>
<td>Musaceae</td>
<td>Musa sp.</td>
<td>SH, HPH</td>
<td>1</td>
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<tr>
<td>Myrtaceae</td>
<td>Psidium guajava L.</td>
<td>EFN, SH</td>
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<tr>
<td>Phytolaccaceae</td>
<td>Hilleria latifolia Lam.</td>
<td>HPH</td>
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<td>Piperaceae</td>
<td>Piper guineensis Schum. et Thonn.</td>
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<td>Posaceae</td>
<td>Phyllostachys sp.</td>
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<tr>
<td>Rubiaceae</td>
<td>Morinda lucida Benth.</td>
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<td>1</td>
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<tr>
<td></td>
<td>Psychotria latistipula Benth.</td>
<td>HPH</td>
<td>1</td>
</tr>
<tr>
<td>Rutaceae</td>
<td>Fagala macrophylla Engl.</td>
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<tr>
<td>Vitaceae</td>
<td>Cyphostemma adenopodium Desc.</td>
<td>EFN, HPH</td>
<td>1</td>
</tr>
</tbody>
</table>

**Fig 1:** Percentage of occupation baits by local ants in non-invaded and by *W. auropunctata* in rural area in southern Cameroon.
Fig 2: Percentage of occupation of nesting resources by local ants in non-invaded and by *W. auropunctata* in rural area in southern Cameroon.

**Conclusion**

This study results emphasize on the ability of the little fire ant, *W. auropunctata* to monopolize feeding and nesting resources in introduced area unlike native ant species. Extrafloral nectaries produced by some plants and honeydew producing hemipterans (HPH) provide crucial resource during the invasive process and facilitate the introduction and dispersion in surrounding areas by invasive ants. As disturbance specialist, invasive ants can nest in different substrates compared to native specialist ants. Human activities are responsible for the invasive success by disturbing environment and providing vacant niche for invasive species. There is an urgent to seek for solutions to stop invasive ant expansions and their negative effects on agricultural production.

**Reference**

4. Banks WA, Williams DF. Competitive displacement of *Paratrechina longicornis* (Latreille) (Hymenoptera: