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► **To cite this version:**

Stanislas Talaga, Jacques H.C. Delabie, Olivier Dézerald, Alex Salas-Lopez, Frédéric Petitclerc, et al.. A bromeliad species reveals invasive ant presence in urban areas of French Guiana. *Ecological Indicators*, 2015, 58, pp.1-7. 10.1016/j.ecolind.2015.05.027 . hal-02095569

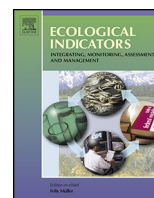
HAL Id: hal-02095569

<https://hal.umontpellier.fr/hal-02095569v1>

Submitted on 11 Jul 2019

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A bromeliad species reveals invasive ant presence in urban areas of French Guiana



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ARTICLE INFO

Article history:

Received 29 November 2014

Received in revised form 18 March 2015

Accepted 11 May 2015

Keywords:

Aechmea aquilega

Bioindicators

Non-specific ant–plant relationships

Surrogacy

Tank bromeliads

Urban ecology

ABSTRACT

Tank bromeliads, frequently associated with ants, are considered 'biodiversity amplifiers' for both aquatic and terrestrial organisms, and thus have a high ecological value. The focal species of this study, *Aechmea aquilega*, sheltered the colonies of 12 ant species in a Guianese rural habitat where *Odontomachus haematodus*, associated with 60% of these plants, was the most frequent. Unexpectedly, the ant species richness was higher in a compared urban habitat with 21 species, but two synanthropic and four invasive ants were noted among them. Consequently, we conducted baiting surveys (on the ground, on trees and on trees bearing *A. aquilega*) as well as complementary surveys using different sampling modes in urban areas to test if *A. aquilega* is a surrogate revealing the presence of certain invasive ants. During the baiting survey, we recorded four Neotropical and eight introduced invasive ants out of a total of 69 species. Of these 12 invasive species, five were noted by baiting *A. aquilega* (including two only noted in this way). A bootstrap simulation permitted us to conclude that *A. aquilega* significantly concentrates certain species of invasive ants. This was confirmed by complementary surveys, where we did not record further species. We conclude that baiting on trees bearing large epiphytes in human-modified, Neotropical areas is a relevant complement to the early detection of invasive ants.

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1. Introduction

Global trade has greatly contributed to the dispersal of plants and animals whose introduction into new habitats generally results in their death or a low rate of survival as they are unable to adapt. Still, some of them have become invasive, constituting an important threat to biodiversity in their introduced range because they can eliminate native species through resource pre-emption and/or direct competition, and, so, disrupt ecosystem functions. This has economic repercussions due to the costs of control measures (Clavero and Garcia-Berthou, 2005; Shogren and Tschirhart, 2005).

Ants are among the most widespread and harmful invasive taxa because they occupy a central place in the functioning of

ecosystems. This is due to their abundance as they constitute one of the largest fractions of the animal biomass and play different roles in food webs since they can be herbivores, generalists, scavengers or predators. In natural conditions, ants coexist in well-organized communities regulated by competition and predation at both the intra- and inter-specific level. Yet, among invasive ants, so-called 'unicolonial species' form spatially vast and competitively dominant supercolonies over large geographical distances (Holway et al., 2002; Moffett, 2012). Thanks to their huge colonies, they lower the species richness and abundance of native ants through exploitation and interference competition so that they can disrupt the arthropod community structure with subsequent repercussions on the entire ecosystem (Holway et al., 2002).

Therefore, a major challenge is to develop predictive management strategies based on understanding the processes behind these invasions. The period just following the introduction of a potentially invasive species is central to that understanding. This is particularly true for insects which, due to their small size, are

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difficult to detect, so that their presence is generally discovered once the invasive process is already well underway or completed. Because most invasive taxa, including ants, are first introduced into urban areas through maritime harbors or airports and along roads (Holway et al., 2002; Laurance et al., 2009), the early detection of ants in cities is a critical component of environmental management. Yet, the ecological requirements of some potentially invasive ants means that their occurrence can be missed when researchers use a conventional sampling technique, especially when these ants first congregate in certain habitats where, in fact, they can be likened to the ‘Trojan Horse’.

Because epiphytes abound in the trees that grow in some Neotropical cities and because epiphytes favor the installation of numerous ant species (Davidson and Epstein, 1989; Dejean et al., 1995; Blüthgen et al., 2000), we hypothesized that large epiphytic plants which commonly form habitats for insects can be “surrogates” for the occurrence of invasive ants prior to their spread. “Surrogacy”, or how easily recorded taxa predict the presence of other taxa, can constitute a useful tool in conservation planning (Warman et al., 2004) and could also be used to detect the recent introduction of potentially invasive ants (see also Addison and Samways, 2006, for artificial surrogate habitats).

Tank bromeliads (Bromeliaceae) are flowering plants comprised of 59 genera and some 3140 species native mainly to the Neotropics (Givnish et al., 2011). The interlocking leaves of tank bromeliads form wells that collect rainwater (from a few milliliters to a few liters), leaf litter and other organic detritus. The rosettes of these plants permit numerous opportunistic ant species to profit from the moist habitat. Most ant-bromeliad associations are not species-specific (Blüthgen et al., 2000), but specialized associations do exist (Dejean et al., 1995). In this context, the aim of this study was to evaluate whether tank bromeliads can reveal ant invasions in Neotropical cities. Tank bromeliads are frequently found in human-modified, Neotropical areas, particularly when those areas are close to the seaside, rivers, or lakes, or situated at high, humid altitudes (Richardson et al., 2000; Serramo Lopez et al., 2009; Cach-Pérez et al., 2013; here *Aechmea aquilega*). So, we first sought to assess whether they point to the presence of synanthropic and invasive ants in urbanized areas of French Guiana, all situated along the coast. Second, we determined if these ant species are outcompeted by native species in a surrounding rural area. Third, we looked for new approaches permitting us to improve the conventional baiting sampling technique so as to detect as effectively as possible the presence of invasive ants by extending the survey to include trees, particularly those bearing an *A. aquilega* cluster. Further surveys using different sampling techniques rounded out this approach.

2. Materials and methods

2.1. The focal taxa

A. aquilega, found from Costa Rica to Brazil, usually forms massive clumps of epiphytes on old trees, but can also grow as a geophyte. This large species (60–120-cm in height; Mori et al., 1997) has tightly interlocking leaves that form a highly compartmented rosette creating a tank (or phytotelm) that collects water and organic detritus and provides a habitat for aquatic micro- and macro-organisms (Carrías et al., 2014).

2.2. Study areas and field surveys

2.2.1. Ants associated with *A. aquilega*

Between 2011 and 2013, we studied the ants associated with 45 mature *A. aquilega* in an urban area (each randomly selected in a city block of Sinnamary, French Guiana; 05°22′39″N 52°57′35″W), and

26 others in a rural habitat situated 5 km away, along 6 km of a dirt road (*route de l’Anse*) lined with 10–30 m-tall trees. In both areas, *A. aquilega* abound as epiphytes, with most individuals growing at a height of 3–6 m on different tree species. The sampling area in each environment extended over a surface of ca. 45 ha.

We used a ladder to reach the selected *A. aquilega* individuals and removed them from their substrates using a hack saw and then placed each of them into a plastic bag which was sealed to avoid contamination during transport to the laboratory. There, each individual was carefully inspected and taken apart; each leaf was torn from the base starting from the outermost leaf and working inward, allowing us to collect entire ant colonies installed between the leaves among the detritus accumulated by the plant.

2.2.2. Baiting survey to test if *A. aquilega* is a surrogate helpful in detecting invasive ants

To detect as effectively as possible the presence of invasive ants, we used a conventional sampling technique consisting of baiting ants with, each time, a series of two 2-ml Eppendorf colorless microtubes (one containing pieces of cotton imbibed with diluted honey and the other containing pieces of canned sardines in oil). Each time, after 30 and then 60 min, the ants occupying the baits and those patrolling all around were collected using an aspirator.

The survey was conducted in Cayenne (4°55′59″N; 52°19′59″W), Kourou (05°09′30″N; 52°38′34″W) and Sinnamary, three cities in the littoral zone of French Guiana (white sand deposits) and situated along a river. Less than 95 km (as the crow flies) separate Cayenne from Sinnamary, with Kourou located almost midway. First, we placed 30 pairs of baits on the ground separated by an interval of more than 20 m in Cayenne (the airport; the heliport; the tarmac of the harbor; the marina; and at the base of the building of the Customs Office in the harbor), in different city blocks of the *Vieux Bourg* of Kourou (areas not far from the marina) and Sinnamary (in different city blocks; more than 100 m from each other). Second, in Kourou and Sinnamary, we used the same type of sampling technique, placing the baits at more than 2 m in height on the trunks of 30 tall trees (>15 m), mostly mango (*Mangifera indica*) and mombin (*Spondias mombin*), both Anacardiaceae, and *Inga* spp. (Mimosoideae). These trees were chosen haphazardly in different city blocks. Third, to verify the ability of *A. aquilega* to concentrate invasive ant species, the same survey was conducted in Sinnamary on 30 other large trees bearing an *A. aquilega* cluster (almost all were mango trees) and situated in different city blocks than the previous trees or in different distant parcels of the same block (with a distance of more than 75 m between two trees). A complementary survey was conducted in the three cities. We firstly prospected by sight along the grassy roadsides of different city blocks, totalizing in each city more than 5 km. Only the workers of infrequent species were gathered (using an aspirator) for further identification. Second, we sampled ants from 20 plots (6 m × 3 m; 18 m²) situated in grassy areas in different city blocks. Sampling was standardized by spending one man-hour per plot carefully searching for ants in all suitable microhabitats: the leaf litter including all hollow, rotten twigs; dead wood; humus and the bare ground. Third, we conducted a baiting survey on trees smaller than in the previous survey (i.e., 5–12 m in height). Also, in the *Vieux Bourg* in Kourou, we baited the only nine reachable mango trees bearing an *A. aquilega* cluster.

Voucher specimens of the ants were identified and deposited in the *Laboratório de Mirmecologia* collection (acronym: CPDC), Cocoa Research Centre (Ilhéus, Bahia, Brazil).

2.3. Statistical comparisons

We compared the ant diversity in the two habitats using Shannon’s diversity *t*-test (PaST software; diversity statistics), and the

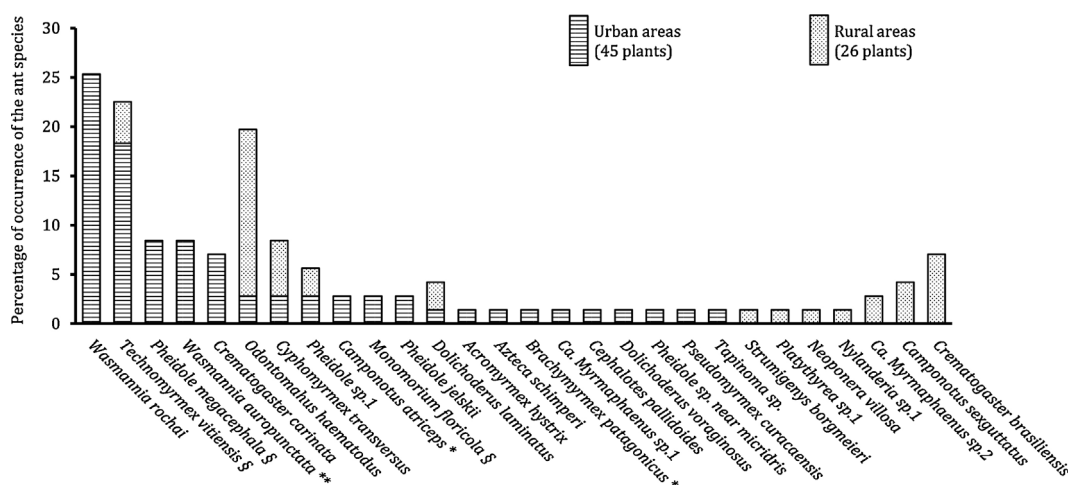


Fig. 1. Comparison of the percentages of occurrence of ant species associated with *Aechmea aquilega* in urban versus rural habitats in the region of Sinnamary, French Guiana. *: synanthropic species; §: introduced invasive species; **: Neotropical invasive species.

ant communities using the Permutational Multivariate Analysis of Variance (PERMANOVA; R software; R Development Core Team, 2013).

The aim of the baiting survey was to test the relative contribution of each of the 10 baiting situations to the total number of invasive ant species recorded in the area. Using R software, we conducted a bootstrap simulation where we “sampled” with replacements the 10 baiting situations. From these simulations, we counted the number of species, and the procedure was repeated 10,000 times. We then split the 10,000 simulations into two groups, one where the *A. aquilega* situation was sampled at least once and a second where it was not sampled at all. Finally, we tested the differences in species number between these two groups with a non-parametric Wilcoxon rank sum test with the continuity correction.

3. Results

3.1. Comparing the ant fauna associated with *A. aquilega* between a rural and an urban area

In all cases, we noted the presence of ants between the base of the *A. aquilega* and the bark of the host trees. A total of 56 out of the 71 *A. aquilega* sampled (79%) sheltered, between their leaves, ant colonies belonging to 28 species and five subfamilies (Fig. 1 and Supplementary Appendix A).

A comparison of the percentages of occurrence of these ant species illustrated the difference in their distribution between the rural and urban areas (12 versus 21 species, respectively; Fig. 1). Indeed, the difference in ant species richness was significant (Shannon’s diversity t -test: $t=3.66$; $df=280$; $P=0.0003$) and the ant assemblages were significantly different between the two sites (PERMANOVA: $N=54$; $F=15.05$; $P=0.0001$).

Odontomachus haematodus was by far the most frequent species in the rural area where it occupied 60% of all of the sampled plants sheltering ants. We noted that elementary nests (the colonies are composed of multiple nests) of this species were installed both between the leaves of several adjacent *A. aquilega* individuals and between their shoots and the bark of the host trees.

3.2. Baiting survey to test if *A. aquilega* is a surrogate helpful in detecting invasive ants

During the baiting survey, we recorded 69 ant species, including 12 well known invasive species, four of which are Neotropical and

are invasive in human-disturbed areas of their native range and elsewhere where they were introduced through human transport; the eight others were introduced (Table 1 and Supplementary Appendix A). Among the introduced invasive ants, five species were recorded during baiting on the ground (i.e., *Monomorium floricola*; *Paratrechina longicornis*; *Tapinoma melanocephalum*; *Tetramorium lanuginosum*; and *Tetramorium simillimum*); two of them, *M. floricola* and *Ta. melanocephalum*, were also recorded on trees. *Cardiocondyla obscurior* was only detected through baiting on trees, and two more species, *Pheidole megacephala* and *Technomyrmex vitiensis*, only by baiting on trees bearing an *A. aquilega* cluster; the latter trees sheltered five invasive species, four of them introduced (Table 1).

Furthermore, the probability of detecting an introduced invasive ant species was particularly high on trees bearing an *A. aquilega* cluster compared to the other situations. Each time the “*A. aquilega* situation” was included in the simulated sample, the number of invasive species was significantly higher than simulations where the “*A. aquilega* situation” was not included (Fig. 2; Wilcoxon rank sum test: $W=2,251,583$; $N=10,000$; $P<2.2e-16$).

The complementary survey permitted us to again note *Pa. longicornis* and *Ta. melanocephalum* among the introduced invasive ants, plus a tramp species, *Cardiocondyla wroughtoni* (Seifert, 2003).

4. Discussion

4.1. Comparing the ant fauna associated with *A. aquilega* between a rural and an urban area

Overall, one can note a convergence between the ant assemblage found in the rural area studied and that of Venezuelan tank bromeliads (Fig. 1; Blüthgen et al., 2000) as *O. haematodus* was the most frequent species, *Cyphomyrmex* spp. abounded, and *Dolichoderus laminatus*, *Neoponera villosa*, and species of the genera *Nylanderia*, *Pheidole* and *Platythyrea* were also recorded. The dominance of *O. haematodus* is reminiscent of the *N. villosa* association with *Aechmea bracteata* in Mexico (Dejean, 1990). Because these two ponerine ant species can also nest in rotten logs or branches lying on the ground, a convergence likely exists where a kind of “local tradition” causes the queens to select these bromeliads as nesting sites. This type of local tradition has also been noted in *Odontomachus hastatus* and social wasps (Wenzel, 1996; Dejean et al., 1998; Gibernau et al., 2007), experimental studies having shown that such host plant selection is related to an imprinting process (Djéto-Lordon and Dejean, 1999).

Table 1

Comparison of ant species recorded in three French Guianese cities using baits (30 pairs of baits each time). *: synanthropic species; ‡: introduced tramp species (not invasive); §: introduced invasive species; **: Neotropical invasive species; #: two associated ant species (parabiosis) which build ant-gardens containing several epiphytes, including the tank bromeliad *Aechmea mertensii*; †: baits on trees bearing *Aechmea aquilega* in Kourou; total: 69 ant species.

Ant species	Baiting on the ground (210 cases)							Baiting on trees (90 cases)		
	Cayenne harbor	Cayenne heliport	Cayenne marina	Cayenne airport	Cayenne customs	Kourou city	Sinnamary city	Kourou trees	Sinnamary trees	† <i>A. aquilega</i>
<i>Azteca cf. chartifex</i>	0	0	0	0	1	0	0	0	0	1
<i>Azteca instabilis</i>	0	0	0	0	0	0	0	0	1	0
<i>Azteca schimperi</i>	0	0	0	0	0	0	0	0	0	1
<i>Azteca</i> sp.1	0	0	0	0	0	0	0	0	1	0
<i>Brachymyrmex patagonicus</i> *	0	1	1	0	1	1	1	0	0	1
<i>Brachymyrmex</i> sp.1	0	0	0	0	0	0	0	0	1	0
<i>Camponotus atriceps</i> *	0	0	0	0	0	0	0	0	1	1
<i>Camponotus blandus</i>	0	1	1	0	1	0	1	0	0	0
<i>Camponotus crassus</i>	0	0	0	0	0	0	0	1	1	1
<i>Camponotus fastigatus</i>	0	1	0	0	0	0	0	1	0	0
<i>Camponotus femoratus</i> #	0	0	0	0	0	0	0	0	0	1
<i>Camponotus</i> (<i>Myrmaph</i>). sp. 1	0	0	0	0	0	0	0	0	1	1
<i>Camponotus melanoticus</i>	0	0	0	0	0	1	1	0	0	0
<i>Camponotus renggeri</i>	0	0	0	0	0	0	0	0	1	0
<i>Camponotus rufipes</i>	0	0	0	0	0	1	1	1	0	0
<i>Camponotus senex</i>	0	0	0	0	0	1	0	0	0	0
<i>Camponotus sexguttatus</i> *	0	0	0	0	1	0	0	1	0	0
<i>Cardiocondyla minutior</i> ‡	0	0	1	0	0	0	1	1	0	0
<i>Cardiocondyla obscurior</i> §	0	0	0	0	0	0	0	1	0	0
<i>Cephalotes pallidoides</i>	0	0	0	0	0	0	0	1	0	1
<i>Cephalotes</i> sp.1	0	0	0	0	0	0	0	0	1	0
<i>Crematogaster abstinens</i>	0	0	1	1	0	1	0	1	0	0
<i>Crematogaster carinata</i>	0	0	1	0	0	0	0	0	1	1
<i>Crematogaster curvispinosa</i>	0	0	0	0	0	0	0	1	0	0
<i>Crematogaster erecta</i>	0	0	0	0	0	0	0	1	0	0
<i>Crematogaster levior</i> #	0	0	0	0	0	0	0	0	0	1
<i>Crematogaster</i> sp.1	0	0	0	0	0	0	0	0	1	0
<i>Crematogaster tenuicula</i>	0	0	0	0	0	0	1	0	0	0
<i>Cyphomyrmex transversus</i>	0	0	0	0	0	0	0	0	0	1
<i>Daceton armigerum</i>	0	0	0	0	0	0	0	0	1	0
<i>Dolichoderus laminatus</i>	0	0	0	0	0	0	0	0	0	1
<i>Dolichoderus voraginosus</i>	0	0	0	0	0	0	0	0	0	1
<i>Dorymyrmex brunneus</i> *	0	0	0	0	0	1	1	0	0	0
<i>Dorymyrmex pyramicus</i> *	0	0	0	0	0	1	1	0	0	0
<i>Ectatomma brunneum</i> *	0	0	0	1	0	0	1	0	0	0
<i>Monomorium floricola</i> §	0	0	1	0	1	0	0	1	0	1
<i>Neoponera villosa</i>	0	0	0	0	0	0	0	0	0	1
<i>Nylanderia fulva</i> **	0	0	1	1	0	0	0	0	0	0
<i>Nylanderia</i> sp.1	0	0	0	0	0	0	1	0	1	0
<i>Odontomachus haematodus</i> *	0	0	0	0	0	0	1	1	0	1
<i>Paratrechina longicornis</i> §	1	1	1	1	1	0	1	0	0	0
<i>Pheidole fallax</i> *	1	1	1	1	1	1	1	0	0	0
<i>Pheidole Diligens</i> group sp.	0	0	1	0	0	0	0	0	0	0
<i>Pheidole jelskii</i> *	0	0	0	0	0	1	1	0	0	0
<i>Pheidole megacephala</i> §	0	0	0	0	0	0	0	0	0	1
<i>Pheidole cf. micridris</i>	0	0	0	0	0	0	0	0	0	1
<i>Pheidole radoszkowskii</i>	0	0	0	0	0	1	1	0	0	0
<i>Pheidole Flavens</i> group sp.1	0	0	0	0	0	1	1	1	0	1
<i>Pheidole Flavens</i> group sp.2	0	0	0	0	0	0	0	1	1	1
<i>Pheidole</i> sp.3	0	0	0	0	0	0	0	0	1	0
<i>Pheidole synamarta</i>	0	0	0	1	0	0	0	0	0	0
<i>Platythyrea sinuata</i>	0	0	0	0	0	0	0	0	1	0
<i>Pseudomyrmex curacaensis</i>	0	0	0	0	0	0	0	0	1	1
<i>Pseudomyrmex gracilis</i>	0	0	0	0	0	1	0	1	1	1
<i>Pseudomyrmex oculatus</i>	0	0	0	0	0	0	0	0	1	0
<i>Pseudomyrmex simplex</i>	0	0	0	0	0	0	0	0	1	0
<i>Pseudomyrmex</i> sp.1	0	0	0	0	0	0	0	0	1	0
<i>Pseudomyrmex termitarius</i>	0	1	0	0	0	1	1	0	0	0
<i>Solenopsis</i> (<i>Diplorhopt.</i>) sp.	0	0	0	0	0	0	0	0	0	1
<i>Solenopsis geminata</i> **	0	0	1	0	0	0	1	0	0	0
<i>Solenopsis globularia</i> *	0	1	0	1	1	1	0	0	0	0
<i>Solenopsis saevissima</i> **	1	1	1	1	1	1	1	0	0	0
<i>Tapinoma melanocephalum</i> §	0	0	1	0	0	0	1	0	1	1
<i>Tapinoma</i> sp.1	0	0	0	0	0	0	0	1	1	1
<i>Technomyrmex vitiensis</i> §	0	0	0	0	0	0	0	0	0	1
<i>Tetramorium lanuginosum</i> §	0	0	0	0	1	0	0	1	0	0
<i>Tetramorium simillimum</i> §	0	0	0	0	0	1	0	0	0	0
<i>Wasmannia auropunctata</i> **	0	0	0	0	0	0	1	1	0	1
<i>Wasmannia rochai</i>	0	1	0	1	0	0	0	1	0	1
No. of species	3	9	13	9	10	16	22	19	22	28
Total No. of invasive species	2	2	6	3	4	2	5	4	1	5
No. of introduced invasive species	1	1	3	1	3	1	2	3	1	4

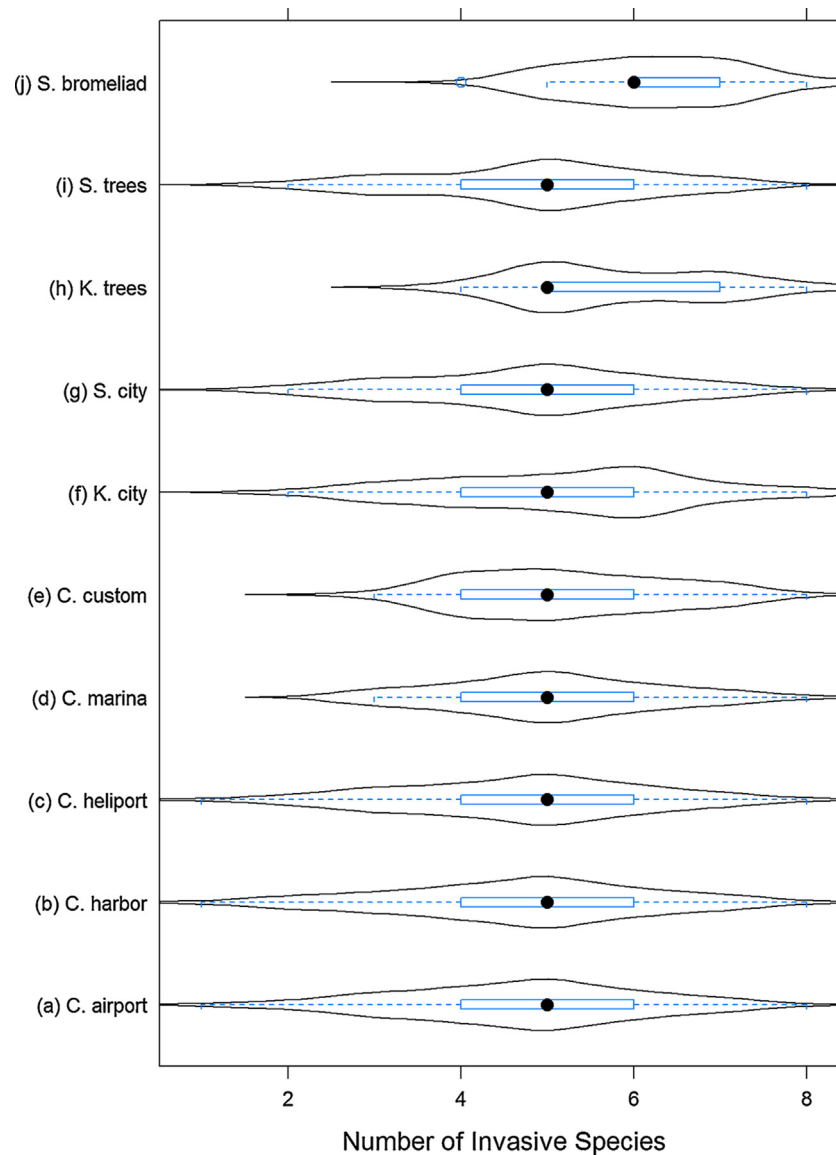


Fig. 2. Comparison of the simulated number of invasive ant species between the 10 baiting situations. A resampling with replacements procedure was conducted resulting in the 10 situations represented by the violin plots (Sarkar, 2008) around box plots which indicate the median (diamond), the 25th and 75th percentiles (white squares), and the minimum and maximum values (dotted lines). For a given situation, we thus had the species number distribution, each value corresponding to a simulation where this situation was included in the 10 baiting situations sampled. Each time the “*Aechmea aquilega* situation” was included in the simulated sample, the number of invasive species was significantly higher than simulations where the “*A. aquilega* situation” was not included (Wilcoxon rank sum test: $W = 2,251,583$; $N = 10,000$, $P < 2.2e-16$). K.: Kourou; C.: Cayenne; S.: Sinnamary; bromeliad: trees bearing an *A. aquilega* bromeliad; large trees sheltering *Aechmea aquilega* clusters.

The much lower level of *O. haematodus* occurrence in the urban area is likely due to anthropogenic disturbances which placed native ants at a disadvantage while favoring synanthropic species, particularly invasive species (Fig. 1 and Supplementary Appendix A). The latter likely lowered native ant richness and abundance through exploitation and interference competition (see Holway et al., 2002). Note that *O. haematodus* colonies, as was observed here, can develop in cities, even nesting in wall crevices or under flower pots (Delabie et al., 1995). Also, this ant species was recently introduced into the Gulf Coast of the USA (MacGown et al., 2014). Note that in the rural area only *Tec. vitiensis* was recorded as an *A. aquilega* associate among the known invasive ants, indicating the beginning of a possible spread.

Three of the species recorded, namely *Wasmannia auropunctata* (Neotropical), *Tec. vitiensis* and *Ph. megacephala* (both of which are introduced species), are invasive ants particularly known for their

negative ecological and agricultural impact (Holway et al., 2002; Bolton, 2007; Delabie et al., 2011; Wetterer, 2012).

4.2. Baiting survey

First, ground baiting permitted us to gather four invasive Neotropical species. *Wasmannia auropunctata* is invasive in many tropical areas where it was introduced; this species, also noted during baiting on trees including those bearing *A. aquilega*, is known to spread in human-disturbed areas of its native range where it can displace other ants (Orivel et al., 2009). *Nylanderia fulva*, a Formicinae native to South America, has invaded the southern USA where it is capable of detoxifying the venom of the introduced fire-ant, *Solenopsis invicta* (LeBrun et al., 2014). Native to Central and South America, *Solenopsis geminata* is now widespread in the Tropics (Holway et al., 2002). Also, *Solenopsis saevissima*, with supercolonies extending over dozens of kilometers, has

negative ecological impacts and has been noted outside its native range (Taber, 2000; Wetterer, 2014a; Lenoir et al., 2015).

Second, during ground baiting, we recorded the five following introduced invasive species. *Monomorium floricola*, also noted on trees including those bearing *A. aquilega*, is a widespread arboreal species native to tropical Asia which can be a house pest (Wetterer, 2010a) or affect the structure of arboreal ant assemblages (Conceição et al., 2014). *Paratrechina longicornis* and *Ta. melanocephalum* (the latter was also noted on trees bearing *A. aquilega*), which have spread worldwide including into cold regions due to their ability to live in houses, are native to the Old World Tropics (Wetterer, 2008, 2009). *Tetramorium lanuginosum*, which was also noted on trees, and *Tet. simillimum* are widespread invasive species, the former is native to tropical East Asia, the latter to Africa (Wetterer and Wetterer, 2004; Wetterer, 2010b). This is the first report of *Tet. lanuginosum* in continental South America although this species has been reported in Central and North America, the Galapagos and several Caribbean islands (Wetterer, 2010b).

Third, *Ca. obscurior* was noted only during tree baiting (Table 1). Native to Southeast Asia, this species is widespread in the Tropics and Subtropics (Seifert, 2003). Note that the other *Cardiocondyla* species recorded, *Ca. minutior* and *Ca. wroughtoni* (Table 1 and Supplementary Appendix B), both native to the Indo-Malayan region, are tramp species widespread in the Tropics and Subtropics but not yet reported as invasive (Seifert, 2003; Wetterer, 2014b).

Fourth, *Tec. vitiensis* and *Ph. megacephala* were only found on trees bearing *A. aquilega*. Already noted in the French Guianese forest, *Tec. vitiensis* is a wide-ranging invasive species likely native to Southeast Asia whose colony growth is favored by colony fission into many nests and by the presence of reproductive worker-queen intercasts in addition to typical queens (Bolton, 2007; Delabie et al., 2011). Native to Africa, *Ph. megacephala* is one of the most widespread invasive ants; its huge supercolonies have a massively devastating effect on the native insect fauna (Holway et al., 2002; Wetterer, 2012).

Therefore, *A. aquilega* baiting provides new information on the presence of invasive ant species as two such species were found only in this way in the present study. Furthermore, of the 12 invasive species noted in total, five were collected by baiting *A. aquilega* and were at a density high enough to show that there is a significant concentration of these species in association with this plant (Fig. 2).

One can note that many invasive ants are ground-nesters, so that *A. aquilega* might be considered inadequate for sheltering colonies of such species. Yet, this is not the case; for example, *Ph. megacephala*, which is mostly a ground-nester, was noted only by baiting *A. aquilega* and not in the other situations tested (Table 1 and Appendices A and B). This might be due to the fact that three native invasive species, *S. saevissima*, *S. geminata* and *W. auropunctata*, are present in all human-disturbed areas, rendering it difficult for an imported species (in this case, *Ph. megacephala*) to establish itself. The few native species able to nest in their presence have adapted to the situation through the use of submissive behaviors and defensive chemicals (Grangier et al., 2007; Roux et al., 2013; Dejean et al., 2015). Nevertheless, *Pa. longicornis* and *Ta. melanocephala* avoid the pressure from these three native, invasive species thanks to their ecological preferences as they mostly nest in direct contact or inside human constructions (Wetterer, 2008, 2009).

5. Conclusion

This survey, mostly conducted in cities where introduced invasive ants are known to nest before spreading to slightly human-disturbed and then undisturbed natural areas (Holway et al., 2002), has highlighted the complementarity between baiting ants on the

ground and on urban trees, particularly those bearing *A. aquilega* clusters. Because *A. aquilega* 'concentrates' certain invasive ants, this global strategy will likely permit researchers to record as exhaustively as possible introduced invasive ants in the areas studied before these ants spread. It appears, therefore, that baiting surveys aiming to detect invasive ant presence in Neotropical cities need to take into account the complementarity between detecting invasive ant species presence on the ground and on trees, particularly those bearing large tank bromeliads and other epiphytes.

Acknowledgments

We are grateful to Andrea Yockey-Dejean for proofreading the manuscript, Alexis Carteron and Frédéric Azémar for technical help, the *Laboratoire Environnement de Petit Saut* for furnishing logistical assistance, and the municipality of Sinnamary (through the Department of the Environment) for permitting us to work inside the city limits. Financial support for this study was provided by an 'Investissement d'Avenir' grant managed by the French *Agence Nationale de la Recherche* (CEBA, ref. ANR-10-LABX-0025). ST's financial support was provided by a PhD fellowship from the *Université Antilles-Guyane*, ASL and OD's financial support was provided by a PhD fellowship from the French *Centre National de la Recherche Scientifique* (CNRS) and the *Fond Social Européen* (FSE). JHCD acknowledges his research grant from CNPq.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2015.05.027>

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