

Traits allowing some ant species to nest syntopically with the fire ant *Solenopsis saevissima* in its native range

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Running title : **Syntopic ants of *Solenopsis saevissima***

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Abstract Supercolonies of the red fire ant *Solenopsis saevissima* (Smith) develop in disturbed environments and likely alter the ant community in the native range of the species. For example, in French Guiana only eight ant species were repeatedly noted as nesting in close vicinity to its mounds. Here, we verified if a shared set of biological, ecological and behavioral traits might explain how these eight species are able to nest in the presence of *S. saevissima*. We did not find this to be the case. We did find, however, that all of them are able to live in disturbed habitats. It is likely that over the course of evolution each of these species acquired the capacity to live syntopically with *S. saevissima* through its own set of traits, where colony size (four species develop large colonies), cuticular compounds which do not trigger aggressiveness (six species) and submissive behaviors (four species) complement each other.

Key words ant community, fire ants, invasive species, *Solenopsis saevissima*, species coexistence, supercoloniality

Introduction

Due to their ubiquity and through their interactions with the fauna and flora, ants occupy a central place in the functioning of entire ecosystems, so that ant invasions are known to generate a succession of negative effects that can have major ecological consequences (Holway *et al.*, 2002). Indeed, most invasive ants develop supercolonies extending over large distances in their introduced range. They are ecologically dominant and exhibit a high level of interspecific aggressiveness, lowering the abundance and diversity of native species and disrupting their community structure as well as that of all arthropods. As a result, five ant species have been listed among the 100 worst invasive species in the world (Holway *et al.*, 2002; Sanders *et al.*, 2003; Helanterä *et al.*, 2009; ISSG, 2013).

Generic conceptual frameworks suggest that the ecological and/or evolutionary changes underlying biological invasions might occur within the native range of introduced species, so that it is now acknowledged that studies are needed in their native ranges (Holway *et al.*, 2002; Lee and Gelembiuk, 2008). Although intra- and interspecific competition in ants limit the expansion of their territories, some species present the supercolony syndrome even in their native range (Orivel *et al.*, 2009; Fournier *et al.*, 2012).

This study focused on a population of the fire ant *Solenopsis saevissima* (Smith) in French Guiana corresponding to a part of its native range that extends from Suriname to northern Amazonia and eastern Brazil where its huge colonies are frequent in human-disturbed areas (Trager 1991; Delabie *et al.*, 2009; Martin *et al.*, 2011). Indeed, *S. saevissima* belongs to an assemblage of recently-diverged taxa, including the well-known invasive fire ants *S. invicta* Buren, *S. richteri* Forel and *S. geminata* (Fabricius) (Ross *et al.*, 2010).

Solenopsis saevissima was introduced into Africa and the Galápagos Islands (Peck *et al.*, 1998; Causton *et al.*, 2006), very likely due to the development of the global transportation network, and so may become a pantropical invasive pest. In tropical areas, its potential threat could be comparable to what is currently happening with regard to *S. invicta* in temperate and sub-tropical climates. Favored by habitat degradation in both its native and introduced ranges, *S. invicta* ecologically dominates the ant community in the former case (Calcaterra *et al.*, 2008), while in the latter case its success is due to the negative impact of human disturbance on native ants rather than a superior competitive ability (King & Tschinkel 2006, 2008). This might explain why it is by far the most studied invasive ant (Tschinkel, 2006; Ascunce *et al.*, 2008; see also recent papers on the negative and positive impacts of this species Chen *et al.*, 2013; Drees *et al.*, 2013; Rashid *et al.*, 2013; Vinson *et al.*, 2013).

In French Guiana, only eight terrestrial ant species [i.e., *Atta sexdens* (L.), *Camponotus blandus* (Smith, F.), *C. melanoticus* Emery, *Crematogaster tenuicula* Forel, *Dorymyrmex pyramicus* (Roger), *Pheidole fallax* Mayr, *S. geminata* and *Wasmannia auropunctata* (Roger)] can nest within a radius of 3 m from a *S. saevissima* mound (Martin *et al.*, 2011; Roux *et al.*, 2013). We thus hypothesized that a shared set of biological, ecological and behavioral traits was selected over the course of evolution which permit these ant species to nest syntopically with *S. saevissima*, competing for food and/or nesting sites, or, alternatively, that each of these species acquired this capacity through its own set of traits.

Materials and methods

Solenopsis saevissima supercolonies can extend over large areas; for instance, in French Guiana a colonial entity composed of many mounds extends over 54 km from Petit Saut (4°59'N; 53°08'W) to Paracou (05°16' N; 52°55' W) (Martin *et al.*, 2011).

Through field-based observations and by using information gathered from the literature (Itzkowitz & Haley, 1983; Torres, 1984; Hölldobler & Wilson, 1990; Perfecto, 1991, 1994; Trager, 1991; Taber, 2000; Morrison, 2002; Orivel & Dejean, 2002; Grangier *et al.*, 2007; Orivel *et al.*, 2009; Roux *et al.*, 2009; Martin *et al.*, 2011), we set up a chart of biological, ecological and behavioral traits (hereafter, "ecological traits" for each ant species and divided these traits into nominal categories (Table 1). The ecological traits and categories correspond to colony size (i.e., small; large; very large; supercolonies), worker size (i.e., smaller or larger than *S. saevissima*; monomorphic or polymorphic), ability to compete for food (i.e., opportunist; extirpator; neither), rhythm of activity (i.e., diurnal or nocturnal), mass recruitment (i.e., presence/absence). We also studied reactions *vis-à-vis* *S. saevissima* workers during dyadic confrontation tests (see Roux *et al.*, 2013) consisting of either the "dear enemy phenomenon" or "nasty neighbor effect" (lesser or greater aggressiveness

toward neighbors than toward strangers, respectively; Temeles, 1994; Müller & Manser, 2007), natural level of aggressiveness, displays of submissive behavior, and whether one of the confronted *S. saevissima* workers experimentally acquired cuticular compounds from workers of the tested species (see Roux *et al.*, 2009; 2013) (Table 2).

Information on the ecological traits concerning the eight ant species able to nest in the vicinity of *S. saevissima* mounds was organized using a fuzzy-coding technique (Chevenet *et al.*, 1994) derived from the fuzzy-set theory (Zadeh, 1965); scores ranged from ‘0’ (no affinity for a trait category) to ‘3’ (high affinity). This technique allowed us to take into account within-species variability in the traits. A species that mostly feeds on other ants and a few other insects, for instance, would be given an affinity of ‘3’ for the feeding category “ant predator” and a ‘1’ for the category “predator”. This procedure allowed us to build a traits matrix that was then analyzed using a Fuzzy Correspondence Analysis (FCA) (Chevenet *et al.*, 1994).

Then, a Principal Component Analysis (PCA) was used to obtain multivariate scores for the dyadic confrontations between *S. saevissima* workers and those from the same eight ant species (here the scores varied between 1 and 7; see details in Table 2). A simultaneous analysis of the ecological traits matrix and the results of the dyadic confrontations between ants was then conducted using a co-inertia analysis (CoA) (Dolédec & Chessel, 1994) to look for covariance between the two data sets. This analysis focuses on co-structure by maximizing the covariance between behaviors during dyadic confrontations and the ecological traits ordination scores in the FCA and PCA analyses (Dray *et al.*, 2003). We measured the correlation between the two sets of data using the RV-coefficient, a multidimensional equivalent of the ordinary correlation coefficient between two variables (Robert & Escoufier, 1976). A permutation test (Dolédec & Chessel, 1994) was used to check the significance of the resulting correlation between the FCA and the PCA analyses. We

carried out 1000 co-inertia analyses of the two datasets (i.e., ecological traits and the results of the dyadic confrontations) after the random permutation of their rows and computed their RV-coefficient values. A P-value is estimated as: $(\text{number of random values} \geq \text{observed value} + 1) / (\text{number of permutations} + 1)$. The test is significant when the P-value is less than the significance level, which means that the observed RV value belongs to a class containing only a few random values among the 1000 possible.

Results and Discussion

A permutation test indicated that the co-inertia between the ecological traits matrix (Table 1) and the results of the confrontations (Table 2) was not significant when *A. sexdens* is taken into consideration nor when *A. sexdens* is excluded as this leaf-cutting ant does not compete for food with *S. saevissima* (Table 2). Hence, there was no correlation between the tested traits of the ants and the results of the confrontation tests. So, we can deduce that the behavioral responses of these eight species to *S. saevissima* individuals do not have a certain degree of similarity, refuting our first hypothesis that a shared set of biological, ecological and behavioral traits was selected over the course of evolution to permit them to nest in the vicinity of its mounds. So, the alternative hypothesis assuming that each of these eight species acquired this ability thanks to its own set of traits is likely (see also Grangier *et al.*, 2007; Le Breton *et al.*, 2007 for species able to nest in the vicinity of *W. auropunctata*). The only trait shared by all these species, including *S. saevissima*, is the ability to develop in disturbed areas.

In addition to the ability to live in disturbed habitats, and independent of colony size, the cuticular compounds of six out of eight of the studied species do not trigger *S. saevissima*

aggressiveness. Indeed, only the cuticular compounds of *S. geminata* (huge colonies) and *C. blandus* (small colonies) trigger *S. saevissima* aggressiveness (Roux *et al.*, 2013).

The size of the colonies is an important trait in thwarting the numerical dominance of *S. saevissima*. For instance, *S. geminata* and *Wasmannia auropunctata* are also supercolonial and their workers are known for their interspecific aggressiveness (Holway *et al.*, 2002). *Solenopsis geminata* shares several traits with *S. saevissima* such as: nest site selection; means of defending food resources; the quick colonization of open, disturbed areas; and high nest density (Perfecto, 1991, 1994; Trager, 1991). Thus, *S. geminata* and *S. saevissima* are in close competition explaining the high level of aggressiveness between workers during confrontations exacerbated by cuticular compounds that trigger aggressiveness (Roux *et al.*, 2013). Although small, *W. auropunctata* workers are fierce competitors for food resources and are able to displace most other ants (Holway *et al.*, 2002; Orivel *et al.*, 2009); they often show submissive behavior when confronted with *S. saevissima* (Roux *et al.*, 2013).

Being a leaf-cutting ant, *A. sexdens* does not compete with *S. saevissima* for food, but its colonies, which can contain 5-8 million workers (Hölldobler & Wilson, 1990), develop numerous foraging trails that radiate out and cross *S. saevissima* territories (AD, pers. obs.). *Atta sexdens* workers are tolerated by *S. saevissima* individuals because their cuticular compounds do not trigger aggressiveness and they systematically enter into thanatosis during confrontations and so are ignored (Roux *et al.*, 2013). *Camponotus melanoticus* forms large, polydomous colonies extending over ca. 200 m and its nocturnally active workers dominate *S. saevissima* individuals in natural conditions (Orivel & Dejean, 2002); moreover, their cuticular compounds do not trigger *S. saevissima* workers' aggressiveness (Roux *et al.*, 2013).

All other four ant species able to live syntopically with *S. saevissima* have comparatively small colonies. *Camponotus blandus* and *D. pyramicus* forage during the

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hottest hours of the day (both are xerotherm species) with little probability of competing with *S. saevissima* which forage 24-hours a day, but mostly at night (Orivel & Dejean, 2002). Yet, while its workers react submissively to *S. saevissima* (Roux *et al.*, 2013), *C. blandus* can aggressively compete with *S. invicta* in Argentina (Calcaterra *et al.*, 2008). *Dorymyrmex pyramicus* workers seldom behave submissively towards *S. saevissima* (Roux *et al.*, 2013). They possess chemical defenses permitting them to harass *S. geminata* (Taber, 2000), while a single individual can attack and disperse a column of army ants (Dejean *et al.*, 2013).

It is likely that *Ph. fallax* workers, which are able to stand up to *W. auropunctata* (Le Breton *et al.*, 2007), attenuated *S. saevissima* aggressiveness through their cuticular compounds and, more importantly, a high rate of submissive behavior (Roux *et al.*, 2013). For *Cr. tenuicula* workers, which only rarely behave submissively, the attenuated *S. saevissima* aggressiveness is likely a result of the workers' cuticular compounds (Roux *et al.*, 2013).

In conclusion, thanks to a specific set of traits, only eight ant species are able to be syntopic with *S. saevissima* in disturbed habitats of its native range. This is important because the ability to displace other species in its native range constitutes one of the major prerequisites for a species to become invasive in areas where it is introduced. Indeed, native species in introduced ranges do not benefit from co-evolutive processes permitting them to resist, so that their vulnerability facilitates the invasiveness of the introduced species.

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Disclosure

The authors have no conflict of interest, including specific financial interests and relationships and affiliations relevant to the subject of this manuscript.

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Table 1. Different biological, ecological and behavioral traits ("ecological traits" in the main text) concerning the eight species able to live syntopically with *Solenopsis saevissima*. Super colon.: supercolonies; smaller, equal: read 'than *S. saevissima* workers'; Eq. polym: polymorphic workers whose size is similar to *S. saevissima* workers; herb.: herbivorous; nectar.: nectarivorous; scav.: scavenger; pred.: predator; opport.: opportunist; extirp.: extirpator; diurn.: diurnal; nocturn.: nocturnal; mass recruit.: presence or absence of mass recruitment.

	Size of colonies				Worker characteristics				Feeding habits					Competing characteristics			Rhythm of activity		Recruitment type	
	Small	Large	Very large	Super colon.	smaller	equal	Eq. polym	Larger polym	Herb.	Nectar.	Scav.	Pred.	Ant pred.	Opport.	Extirp.	None	Diurn.	Noct.	Mass recruit.	absent
<i>D. pyramicus</i>	3	0	0	0	0	3	0	0	0	2	1	1	0	3	0	0	3	0	3	0
<i>S. geminata</i>	0	0	0	3	3	0	1	0	0	3	1	2	0	0	3	0	2	3	3	0
<i>Ca. melanoticus</i>	0	0	3	0	0	0	0	3	0	3	1	2	0	0	3	0	0	3	0	3
<i>Cr. tenuicula</i>	3	0	0	0	3	0	0	0	0	3	1	1	0	3	0	0	3	0	3	0
<i>P. fallax</i>	3	0	0	0	3	1	0	1	0	2	1	1	1	3	0	0	3	3	3	0
<i>W. auropunctata</i>	0	0	2	3	3	0	0	0	0	1	1	2	1	0	3	0	2	3	3	0
<i>Ca. blandus</i>	0	3	0	0	0	0	0	3	0	3	1	1	0	1	2	0	3	0	0	3
<i>A. sexdens</i>	0	0	3	0	1	0	0	3	3	0	0	0	0	0	0	3	2	3	3	0
<i>S. saevissima</i>	0	0	0	3	0	0	3	0	0	3	3	3	0	0	3	0	2	3	3	0

Table 2. Reactions *vis-à-vis* *S. saevissima* workers during confrontation tests (Roux *et al.*, 2013); dear enemy phenomenon (DEP); natural level of aggressiveness (Nat. aggr.); submissive behavior (Sub. Behav.); confrontations with strangers (Strang.) or with nestmates (Nest.). In each case, according to results in Roux *et al.* (2013), we assigned values ranging from 1 (low level) to 7 (very high level) with two intermediary levels. †: Intraspecific interactions for *S. saevissima*. The co-inertia between the ecological traits matrix from Table 1 and the results of the confrontations presented in this table (permutation test) was not significant when *A. sexdens* is taken into consideration (co-inertia RV coefficient = 0.04; P = 0.88) nor when *A. sexdens* is excluded (RV = 0.041; P = 0.86).

	DEP	Nat aggr.	Sub. Behav.	Confrontations	
				Strang.	Nest.
<i>Dorymyrmex pyramicus</i>	7	3	3	5	7
<i>Solenopsis geminata</i>	7	7	3	1	7
<i>Camponotus melanoticus</i>	5	1	3	5	7
<i>Crematogaster tenuicula</i>	3	3	1	7	7
<i>Pheidole fallax</i>	3	5	7	5	7
<i>Wasmannia auropunctata</i>	1	3	7	5	7
<i>Camponotus blandus</i>	1	7	7	1	3
<i>Atta sexdens</i>	1	3	7	5	7
<i>Solenopsis saevissima</i> †	1	7	7	5	3