Biol Invasions
DOI 10.1007/s10530-015-0892-5

ORIGINAL PAPER

Different behavioural strategies among seven highly invasive ant species

Cleo Bertelsmeier · Amaury Avril · Olivier Blight · Amandine Confais · Lise Diez · Hervé Jourdan · Jérôme Orivel · Noémie Saint Germès · Franck Courchamp

Received: 28 September 2014 / Accepted: 31 March 2015

Abstract Ants figure prominently among the worst invasive species because of their enormous ecological and economic impacts. However, it remains to be investigated which species would be behaviourally dominant when confronted with another invasive ant species, should two species be introduced in the same area. In the future, many regions might have suitable environmental conditions for several invasive ant species, as predicted under climate change scenarios. Here, we explored interactions among several highly invasive ant species, which have been shown to have overlapping suitable areas. The aim of this study was to evaluate the performance in interference competition of seven of the world's worst invasive ant species (*Anoplolepis gracilipes*, *Paratrechina longicornis*, *Myrmica rubra*, *Linepithema humile*, *Lasius neglectus*, *Wasmannia auropunctata* and *Pheidole megacephala*). We conducted pairwise confrontations, testing the behaviour of each species against each of the six other species (in total 21 dyadic confrontations). We used single worker confrontations and group interactions of 10 versus 10 individuals to establish a dominance hierarchy among these invasive ant species. We discovered two different behavioural strategies among these invasive ants: three species displayed evasive or indifferent behaviour when individuals or groups were confronted (*A. gracilipes, Pa. longicornis, M. rubra*), while the four remaining species were highly aggressive during encounters and formed a linear dominance hierarchy. These findings contrast with the widespread view that invasive ants form a homogeneous group of species displaying the 'invasive syndrome', which includes generally

---

Electronic supplementary material The online version of this article (doi:10.1007/s10530-015-0892-5) contains supplementary material, which is available to authorized users.

C. Bertelsmeier (✉) · A. Avril · A. Confais ·
N. Saint Germès · F. Courchamp
Laboratoire Ecologie, Systématique & Evolution (ESE),
UMR CNRS 8079, Univ. Paris Sud, Bâtiment 362,
91405 Orsay, France
e-mail: cleo.bertelsmeier@gmail.com

O. Blight
Estación Biológica de Doñana, Consejo Superior de
Investigaciones Científicas, Seville, Spain

L. Diez
Unité d'Ecologie Sociale, Univ. Libre de Bruxelles,
Brussels, Belgium

H. Jourdan
UMR CNRS - IRD - UAPV, Centre IRD Nouméa, Institut
Méditerranéen de Biodiversité et d'Écologie marine et
continentale (IMBE), Aix-Marseille Université, BP A5,
98848 Nouméa Cedex, New Caledonia

J. Orivel
CNRS, UMR Ecologie des forêts de Guyane,
AgroParisTech, CIRAD, INRA, Univ. De Guyane, Univ.
Des Antilles, Campus Agronomique, BP 316,
97379 Kourou Cedex, France

aggressive behaviour. The dominance hierarchy among the four aggressive species may be used to predict the outcome of future competitive interactions under some circumstances. Yet, the existence of several behavioural strategies renders such a prediction less straightforward.

Keywords Invasive ants · Dominance hierarchy · Dominance trade-offs · Dyadic confrontations · Interference competition · Invasive syndrome

Introduction

Biological invasions are one of the greatest threats to biodiversity (Essl et al. 2011; Simberloff et al. 2013). Among invasive species, ants are a particularly prominent group. More than 200 exotic species have been recorded (Suarez et al. 2010), 19 are listed by the IUCN Invasive Species Specialist Group as highly invasive (IUCN SSC Invasive Species Specialist Group 2012) and five are even on the IUCN "100 of the world's worst invasive species" list (Lowe et al. 2000). Invasive ants are often highly aggressive, dominant competitors that displace many native species, through either direct or indirect competition, i.e. interference or exploitation competition (Holway 1999; Rowles and O'Dowd 2007; Carpintero and Reyes-López 2008). During interference competition, two species interact physically by aggressively attempting to exclude one another from particular habitats. Exploitation competition involves the ability of an ant species to locate a resource quickly and remove the resource before the competitors. Taxonomic groups affected by invasive ants include most native ants, many arthropods (spiders, crabs, insects), birds, reptiles, amphibians, mammals and plants (Holway et al. 2002; Lach and Hooper-Bui 2010; Rabitsch 2011; Wittman 2014). However, the impacts and behaviour of many invasive ants, including several species investigated in this study, remain understudied.

Studies using species distribution models have predicted suitable ranges for invasive ants, indicating that they have not yet realized their potential distributions (Fitzpatrick et al. 2007; Roura-Pascual et al. 2009; Bertelsmeier et al. 2013a, b). Models indicate substantial overlaps of potential ranges of different invasive ant species (Bertelsmeier et al. 2015). Indeed, it is likely that these invasive species will be introduced within their suitable ranges in the future, as recent analyses have shown the strong human-mediated component to long-distance dispersal of invasive ants (Suarez et al. 2010; Bacon et al. 2014). In fact, the number of ant introductions could be much higher than the number of detections (Miravete et al. 2014). Therefore it is a realistic future scenario that invasive species with common suitable areas will encounter each other in the field and interact.

So far, it is unclear how sympatric invasive ant species will interact. Invasive ants share many ecological and life-history traits. Together, these traits are often referred to as the "invasive syndrome" (Passera 1994). All of these species form large polygynous colonies, covering extensive territories, and they have very generalist diet, nesting and habitat requirements and foraging strategies (Holway et al. 2002; Lach and Hooper-Bui 2010; Rabitsch 2011). Therefore, it is likely that these invasive ant species will compete for the same resources and displace one another, unlike dominant ants in native communities, which often differ from subordinates in their diet preferences and/or foraging strategies (Arnan et al. 2012). In addition, in native communities interspecific trade-offs, for example in the ability to discover and to defend resources, promote species co-existence. Invasive species, however, are generally thought to avoid these trade-offs by being simultaneously very fast at discovering resources and able to dominate them (Human and Gordon 1996; Holway 1998, 1999). Observations from ranges where two invasive ant species come in contact show competitive exclusion and displacement of one invasive ant by another at a local scale. Examples include the mutual exclusion of *Linepithema humile* and *Solenopsis invicta* in the Southern US (LeBrun et al. 2007), *Li. humile* and *Pheidole megacephala* in Hawaii (Krushelnycky and Gillespie 2010) and Bermuda (Lieberburg et al. 1975), *Li. humile* and *Pachycondyla chinensis* in the US (Spicer Rice and Silverman 2013a) and *W. auropunctata* and *Ph. megacephala* in New Caledonia (Chazeau et al. 2000, Le Breton 2003). However, the aggressiveness of many invasive ants has not been studied yet and it remains to be investigated how these invasive ant species would interact with one another, when introduced in the same area.

The aim of our study was to evaluate the performance in interference competition of seven of the world's worst invasive ant species, testing the behaviour of each species against each of the six other species. All seven species are listed by the IUCN as among the worst invasive ants (IUCN SSC Invasive Species Specialist Group 2012): the big-headed ant (*Ph. megacephala*), the invasive garden ant (*Lasius neglectus*), the Argentine ant (*Li. humile*), the little fire ant (*W. auropunctata*), the yellow crazy ant (*Anoplolepis gracilipes*), the common red ant (*Myrmica rubra*) and the long-horn crazy ant (*Paratrechina longicornis*). We used a classic setup for pairwise confrontations (Errard et al. 2005; Buczkowski and Bennett 2008a; Blight et al. 2010) to test worker and group interactions for each species against the six other ($n = 10$ for each combination). We used both, a dyadic interaction experiment between individual workers because it allowed us to record precisely different types of behaviour (e.g. mandible opening, antennation…) and to a group-level interaction experiment. The latter was used because some fighting strategies are only displayed when individual workers are members of a group.

Methods

Colony collection and maintenance of laboratory colonies

The ants were collected between March and December 2012 in New Caledonia (*A. gracilipes*, *W. auropunctata*, *Ph. megacephala*, *Pa. longicornis*), in Southern France (*Li. humile* and *La. neglectus*), in French Guiana (*W. auropunctata*) and Gembloux, Belgium (*M. rubra*). Details of ant collections are provided in the Supplementary Material (S1). Behavioural assays were conducted between April 2012 and January 2013. Colony fragments were maintained in plastic nest containers (55 × 35 × 25 cm) filled with substrate from the original nesting site (soil, wood, leafs) and contained several tubes of water. The boxes were kept at 24 ± 2 °C with the appropriate soil moisture. The ants were fed daily with a variant of the traditional Bhatkar diet containing a protein mix (whey protein, calcium caseinate and albumin), shown to be superior for the maintenance of laboratory colonies; the exact mixture and preparation is described in Dussutour and Simpson (2008).

Behavioural assays

One-on-one

Individual dominance at interference competition was determined during confrontations of all possible pairs of species among the seven invasive ant species, totalling 21 species interactions. One foraging worker was randomly selected from each of the stock colonies and placed in a small plastic cylinder (diameter 2.5 cm, height 3 cm) which was turned upside down in a petri dish (diameter 5.5 cm, height 1.5 cm) coated with Fluon® to prevent the ants from escaping. The ants were allowed to acclimatize for 2 min before removing the two tubes containing one ant each. Behavioural interactions were videotaped for 5 min. Each of the 21 pairwise combinations was replicated 10 times. Each worker was used only once and the arena was cleaned with 70 % alcohol between two trials to eliminate any pheromones. For this experiment, only minor workers of *Ph. megacephala* were used, the only species in this experiment with two morphological castes.

For both opponents, the occurrence of the following behaviours was recorded: Antennation, mandible opening, physical aggression (worker bites the opponent), chemical aggression (worker sprays formic acid or stings the opponent), being bitten, feigning death, escaping and indifference. We also recorded the final outcome (dead, injured or alive) by the end of the 5 min video recording and the attack initiator. We analysed the relationship between the final outcome and attack initiation for all dyadic confrontations where an aggressive interaction was observed and where the attack initiator could be determined.

Group confrontation

The objective of the group bioassay was to test interference competition between pairs of species in equal groups of ten workers. Because *Ph. megacephala* is a polymorphic species, all opponent species were confronted with both a) ten minor workers of *Ph. megacephala* and b) one soldier and nine minor workers (following the proportions in Kirschenbaum and Grace 2008). Therefore, in total 27 pairwise species interactions were conducted. Ten foraging workers of each species were randomly selected and separated from the stock colonies. The groups were then transferred into two small cylinders coated with Fluon® to acclimatize for 2 min in their respective cylinder before being released simultaneously. The group confrontations were videotaped for 30 min. Ten replicates for each species interaction were conducted, except some interactions involving *A. gracilipes* (six replicates vs. *La. neglectus*, five replicates vs. *Ph. megacephala* without soldier, six replicates vs. *Ph. megacephala* with soldier, seven replicates vs. *Pa. longicornis*). The numbers of alive, injured and dead workers were recorded every minute during the first 5 min and then every 5 min until 30 min, which was considered to be the end of the interaction.

Statistical analyses

A Survival Index (*SI*) was calculated for each species based on the outcome of the group confrontations, according to the formula:

$$SI = (A + 0.5\,I)/N$$

where A is the number of alive workers, I is the number of injured workers and N the number of workers per replicate.

In addition, a Killing Index (*KI*) was calculated for each species based on the outcome of the group confrontations according to the formula:

$$KI = (D + 0.5\,I)/N$$

where D is the number of dead opponents, I is the number of injured opponent workers and N is the number of workers per replicate.

In order to combine the species' ability to survive a confrontation and its ability to kill the opponent in a single index, a dominance index (*DI*) was used, which takes into account both the species' survival and killing rate:

$$DI = KI/(1 - SI)$$

If $DI > 1$, the species kills more opponents than it loses its own workers and when $DI < 1$ it has a greater death $(1 - SI)$ rate than killing rate (*KI*). If the number of workers killed and the number of own workers lost are equal ($SI = 0.5$, $KI = 0.5$), then $DI = 1$. All three indices, *SI*, *KI* and *DI* were calculated based on the outcome after 30 min of interaction.

All analyses were conducted with R v. 2.15.2. Prior to statistical analysis of the differences in *SI, KI* and *DI* among species, all data distributions were examined using the Shapiro–Wilk *W* test for normality. Because the residuals did not conform to a normal distribution, the nonparametric Kruskal–Wallis rank sum test was used, adjusting for multiple comparisons with a Kruskal multiple comparison test of the kruskalmc() function included in the pgirmess package in R. The relation between *SI* and *KI* was tested using a Spearman rank correlation. A principal component analysis of the behaviours displayed during the one-on-one bioassays by the different species was conducted using the ade4 package. A χ^2 test was used to test whether the initiating a fight was associated with a certain outcome of the interaction.

Results

The differences in behaviours across species during one-on-one interactions are represented by a principal component analysis showing simultaneously species and behaviours (Fig. 1). Overall, *Ph. megacephala* and *Li. humile* are mostly associated with 'Physical attack' and 'Being bitten', *La. neglectus* is mostly associated with 'Chemical attack' and 'Mandible opening', *W. auropunctata* with 'Death feigning' and *M. rubra*, *A. gracilipes* and *Pa. longicornis* with 'Indifference' and 'Escaping'.

The outcome of confrontations differed significantly according to whether the ant was the fight initiator or not, with the fight initiator injuring or killing the opponent in a significantly higher proportion of fights (χ^2 (2, 88) = 6.88, $p = 0.03$). Among the individuals that were identifiable as fight initiator, 69 were alive, 8 injured and 11 dead by the end of the interaction. Among those that were attacked, only 54 were alive, while 10 injured and 24 dead. The species that initiated most fights was *La. neglectus*, followed by *Li. humile* and *W. auropunctata* (Fig. 2).

During group interaction of 10 versus 10 workers, we also recorded, after 30 min, the survival of each species according to their opponent, and the survival of that opponent (in percentage, Table 1). For example, *M. rubra* has a very high survival in all confrontations, mostly 100 % or slightly less (row 'MY'), but its opponents have a very high survival, too (column 'MY'), showing that the species is best at surviving but does not often kill its opponents. On the other hand, *W. auropuncta* has also a very high

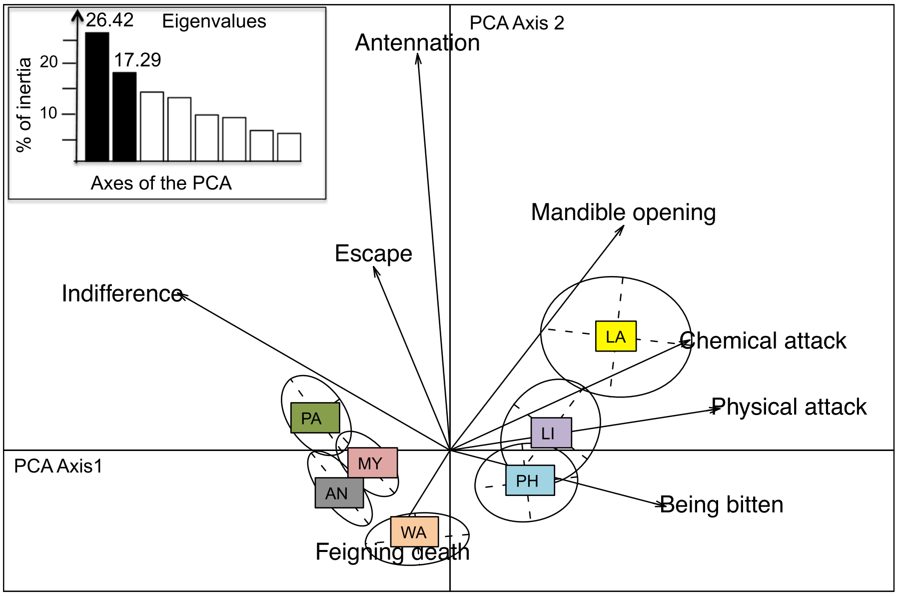

Fig. 1 PCA biplot along the two first principal components, associating species with observed behaviours. In the *upper left corner*, the percentage of inertia of the first axes of the principal component analysis is given in an eigenvalue plot (in *black* for the two first), i.e. the percentage of variation in the multivariate data captured by the representation along those two axes

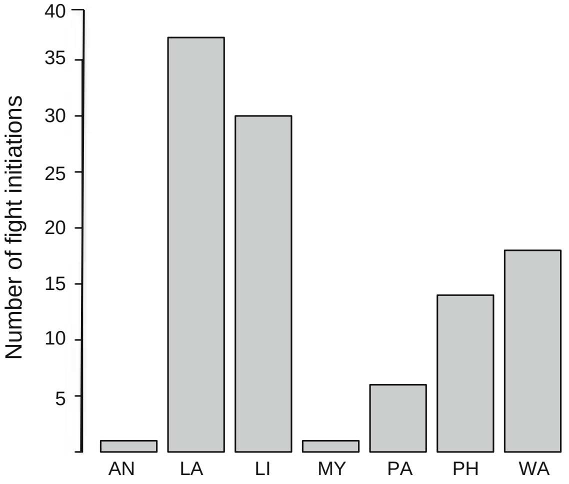

Fig. 2 Cumulative number of fight initiations per species, across 88 confrontations. In the remaining replicates, no attack occurred (106 cases) or the aggressor could not be determined (6 cases). Species names: AN, *Anoplolepis gracilipes*; LA, *Lasius neglectus*; LI, *Linepithema humile*; MY, *Myrmica rubra*; PA, *Paratrechina longicornis*; PH, *Pheidole megacephala*; WA, *Wasmannia auropunctata*

survival (row 'WA') but its opponents have close to 0 % survival (column 'WA'), except *A. gracilipes*, *M. rubra* and *Pa. longicornis*. The latter three species do not dominate over *W. auropunctata* as they too inflict almost no mortality in turn. *Ph. megacephala* has a low survival in most pairwise interactions and has a low killing rate.

We summarized overall *SI* and *KI* per species across interactions (Fig. 3a, b). A Kruskal–Wallis test revealed a significant difference across species, both in *SI* ($\chi^2_{(7)} = 215.51$, $p < 0.0001$; Fig. 3a) and in *KI* ($\chi^2_{(7)} = 114.83$, $p < 0.0001$; Fig. 3b).

We summarized the species' surviving and killing abilities in the *DI* index across interactions (Fig. 4a). A Kruskal–Wallis test showed a significant difference in *DI* across species ($\chi^2_{(7)} = 223.41$, $p < 0.0001$; Fig. 4a). This dominance hierarchy index ranks the species in the following order, although some pairwise differences are not significant (cf Fig. 4a):

> *W. auropunctata* > *La. neglectus* > *M. rubra* > *A. gracilipes* > *Li. humile* > *Pa. longicornis* > *Ph. megacephala* +soldier > *Ph. megacephala* without soldier.

The surviving and killing abilities are not correlated ($r^2 = 0.14$, $p = 0.36$). Thus, we also represented the species' surviving and killing abilities on two separate axes instead of summarizing them in a single index (Fig. 4b). Accordingly, the seven species can be separated into two groups. The first group clusters at

Table 1 Survival of both opponents in dyadic group confrontations

	Opponent							
Survival of focal species	AN	LA	LI	MY	PA	PH	PH+S	WA
AN	NA	68 ± 5	72 ± 4	86 ± 4	99 ± 1	72 ± 5	81 ± 4	99 ± 1
LA	88 ± 3	NA	65 ± 8	86 ± 5	97 ± 2	95 ± 2	90 ± 2	12 ± 5
LI	75 ± 5	10 ± 3	NA	44 ± 6	91 ± 3	79 ± 4	58 ± 5	4 ± 2
MY	100 ± 0	100 ± 0	100 ± 0	NA	100 ± 0	100 ± 0	97 ± 1	91 ± 4
PA	95 ± 2	44 ± 8	54 ± 7	92 ± 2	NA	92 ± 2	93 ± 1	44 ± 8
PH	57 ± 5	4 ± 1	18 ± 3	73 ± 4	85 ± 6	NA	NA	3 ± 1
PH+S	69 ± 2	12 ± 3	32 ± 1	72 ± 5	76 ± 5	NA	NA	7 ± 2
WA	93 ± 1	90 ± 4	97 ± 1	93 ± 3	85 ± 4	98 ± 2	66 ± 6	NA

Values are expressed as the % of survival of the focal species (row) when confronted to the other species (column) ± SE over replicates. The grey shading is proportional to the percentage of surviving individuals

Species names: AN, *Anoplolepis gracilipes*; LA, *Lasius neglectus*; LI, *Linepithema humile*; MY, *Myrmica rubra*; PA, *Paratrechina longicornis*; PH, *Pheidole megacephala*; PH + S, *Pheidole megacephala* with soldier; WA, *Wasmannia auropunctata*

a high *SI* and low *KI* and corresponds to the three species that were associated with the indifference and escaping behaviours (Fig. 1): *M. rubra*, *A. gracilipes* and *Pa. longicornis*. The second group shows a hierarchy from species with high values for both *KI* and *SI* (*W. auropunctata*) to a species with low values for both *KI* and *SI* (*Ph. megacephala*). This latter group is constituted by species that mostly fight (associated with either physical or chemical attacks) and do not show evasive behaviour (Fig. 1). Among those four species, there is a significant linear relationship between *KI* and *SI* ($r^2 = 0.91$, $p < 0.01$).

Discussion

Despite being among the worst global invaders (IUCN SSC Invasive Species Specialist Group 2012), the seven invasive ant species differed greatly in their performance in interference competition. The top dominant competitor was *W. auropunctata* and the least dominant species was *Ph. megacephala*. In addition to the quantitative difference in interference competition, there was a qualitative difference in the type of interactions between species and two distinct behavioural strategies could be observed. Four species (*W. auropunctata*, *La. neglectus*, *Li. humile*, *Ph. megacephala*) interacted aggressively with all other species and displayed behaviours such as mandible opening, chemical and physical attacks. These four species formed a clear linear hierarchy, with the top species excelling at inflicting injuries and causing the death of its opponent, while suffering very low mortality. The lowest ranking species of the four were injured and killed more frequently without being able to injure or kill as much the other species. The three remaining species (*Pa. longicornis*, *M. rubra* and *A. gracilipes*) mostly avoided aggressive interactions by displaying indifference or escaping their opponents, which contrasts with the findings that other investigated invasive ant species are behaviourally dominant (Holway et al. 2002; Rabitsch 2011). Consequently, they had a high survival rate but a low killing rate. Among these three species, it is difficult to establish a 'dominance hierarchy' because in pairwise interactions, the species avoided each other and death or injuries rarely occurred. But how does this evasive group relate to the linear dominance hierarchy among the other four species? For the purpose of interspecific comparison, different types of dominance indices

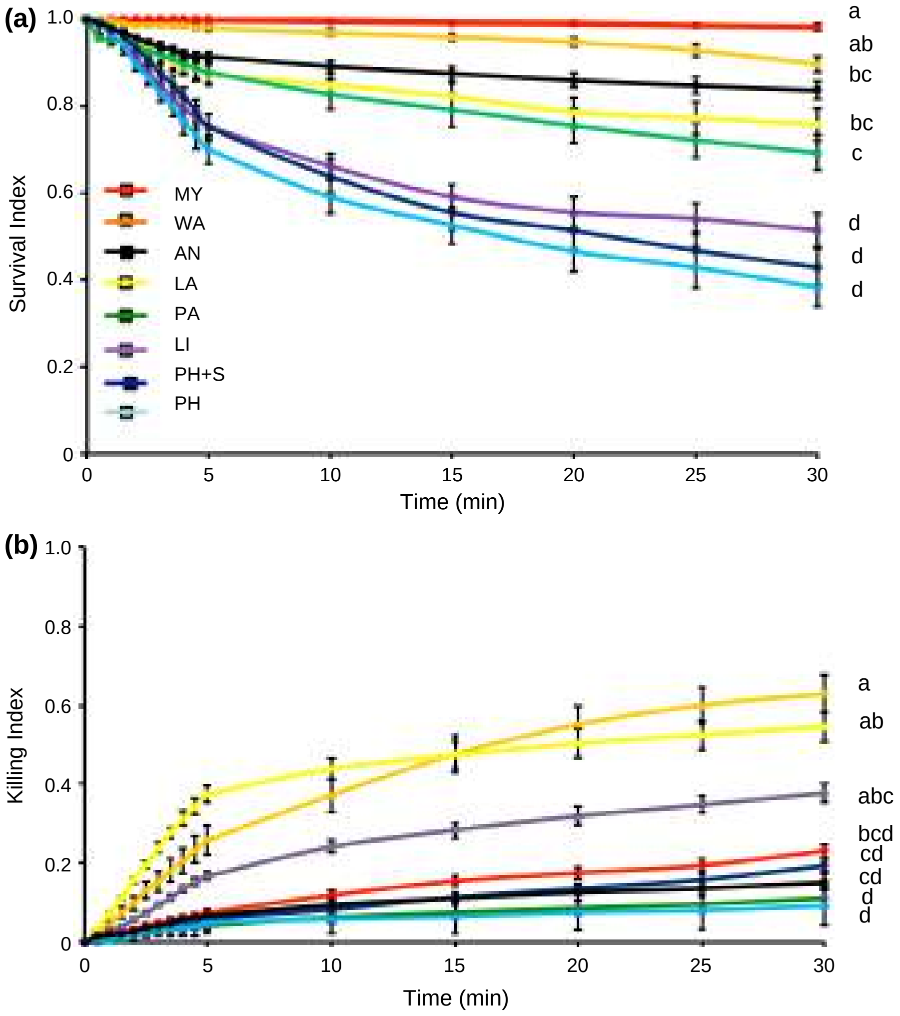

Fig. 3 **a** Survival Index (*SI*) per species over 30 min of observation across interactions with different opponents, **b** Killing Index (*KI*) per species over 30 min of observation across interactions with different opponents. *Different letters* denote significant pairwise comparisons in the post hoc multiple comparison Kruskal–Wallis test (5 % level). Values are given ± SE. Species names: AN, *Anoplolepis gracilipes*; LA, *Lasius neglectus*; LI, *Linepithema humile*; MY, *Myrmica rubra*; PA, *Paratrechina longicornis*; PH, *Pheidole megacephala*; PH + S, *Pheidole megacephala* with soldier; WA, *Wasmannia auropunctata*

exist, which rank the species according different weights to dominant (e.g. killing) or subordinate (dying) behaviour (Bang et al. 2010). We have illustrated the outcome of a single *DI*, which includes both surviving and killing scores. All ranking methods would ‘force’ a ranking among all seven species, with the three evasive species inserted in the linear dominance hierarchy (Fig. 4a). However, that type of forced linear ranking misses the two different behavioural strategies entirely (Fig. 4b). The two distinct behavioural groups correspond to different strategies, one prioritizing the ability to kill competitors and achieving ecological dominance through interference competition, and the other prioritizing survival. The latter, less aggressive group, may either succeed in invading native communities through efficient exploitation competition, or is more aggressive only when confronted to native, less competitive species.

Ant community studies classically define the dominance score of a species as the percentage of time it initiates an attack or when its presence elicits avoidance in an encounter with another species (Fellers 1987; Cerdá et al. 1997; Arnan et al. 2012). Applying this definition to the seven invasive ant species here, the three evasive species would be ranked lowest (Fig. 2b). Given their high overall survival and the fact that all three species win pairwise interactions against *Ph. megacephala*, this classic DI seems inadequate here. Previously, species have also been ranked according to their mean survival in confrontations in laboratory experiments (Kabashima

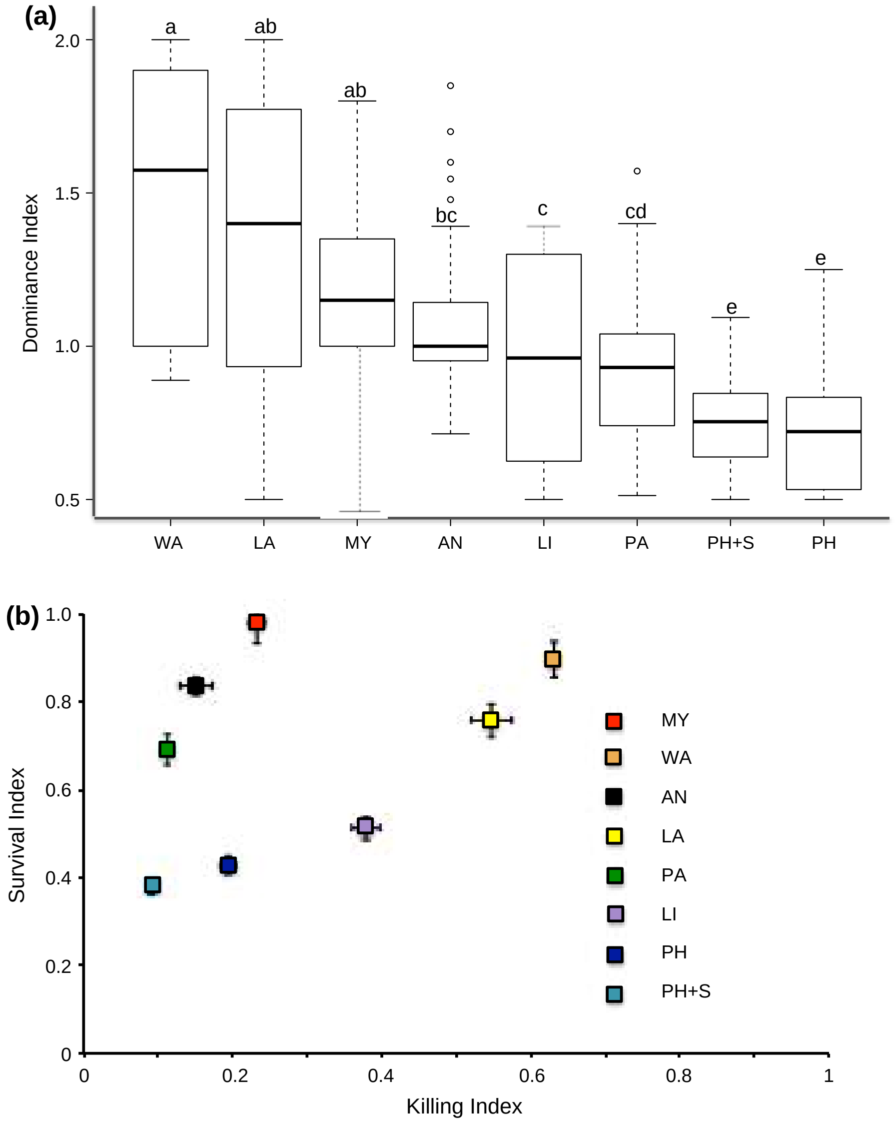

Fig. 4 **a** Dominance Index (*DI*), **b** mean Survival Index (*SI*) ± SE, mean *KI* ± SE by the end of the 30 min observation period, with the same color code as the previous figures. Species names: AN, *Anoplolepis gracilipes*; LA, *Lasius neglectus*; LI, *Linepithema humile*; MY, *Myrmica rubra*; PA, *Paratrechina longicornis*; PH, *Pheidole megacephala*; PH + S, *Pheidole megacephala* with soldier; WA, *Wasmannia auropunctata*

et al. 2007; Kirschenbaum and Grace 2008). This ranking, however, would greatly improve the score of the three species of the evasive group because of their high overall survival. But this ranking does not take into account the species' rather poor attacking and killing abilities. Therefore, it appears inadequate, as well, for summarizing the dominance relationships among the seven species studied.

In the single worker interactions, we observed behavioural differences among the four species in the linear hierarchy include the use of mostly physical defences by the two lowest ranking species, *Ph. megacephala* and *Li. humile* versus chemical defence for the two higher ranking species. Surprisingly, the highest-ranking species in our study, *W. auropunctata*, displayed death-feigning behaviour in interactions where it ultimately won. This is remarkable given the observation by Blight et al. (2010) of death feigning by *Li. humile* when it was losing the confrontation. A further interesting result is that the fight initiator was more likely to dominate the opponent. It would be interesting to further investigate the context-dependence of these behaviours, as previous research has indicated that the behavioural strategy may not be fixed (Sagata and Lester 2009).

In the group confrontations, different species differed remarkably fast in their mean *SI* and *KI* (Fig. 3). This demonstrates that the results are stable over time and no variation in relative dominance of the different species occurs over the time of the experiment (30 min). An unexpected result was that the addition of a soldier to *Ph. megacephala* groups did not have a significant effect on their survival or killing rate. The soldier displayed passive behaviour and did not engage preferentially in confrontations. As soldiers are bigger than minors and more costly to produce for the colony, one would expect a benefit during confrontations. We used the same minor-soldier ratio that has been used in previous studies (Kirschenbaum and Grace 2008), but it is possible that more than one soldier, or larger interacting groups, are needed to elicit more active responses from the soldiers. However this apparent lack of a soldier effect has been observed in native *Pheidole* species displaying ill-adapted defence behaviour towards the invasive *W. auropunctata* (Le Breton et al. 2007). The way in which they seize *W. auropunctata* workers does not protect them from being stung (Le Breton 2003). Maybe interference competition is not the key to invasiveness in *Ph. megacephala*. Is possible that *Ph. megacephala* does not dominate invaded ant communities through direct physical interactions (interference competition) but by raiding their colonies (Dejean et al. 2008)

The study strictly followed classical protocols in assessing interspecific dominance, but this approach includes some limitations. Among them, the observed behaviour could be dependent on the particular population of the invasive species that we used and differ in other populations of the same species. Previously, such differences in aggressiveness towards native species have been observed between two supercolonies of Argentine ants (Abril and Gomez 2011). For our experiments, *M. rubra* samples were collected in the native range of the species. We did not observe passivity in this species, which had the fourth largest killing index, but it would be interesting to investigate differences between native and invasive populations in future experiments. In addition, the laboratory settings under which we carried out the confrontations may have created some unrealistic conditions. In particular, the confrontations were carried out on a "neutral" territory and the defence behaviour of ants can depend strongly on the proximity to the nest (Hölldobler and Lumsden 1980). In the future, it would be very interesting to conduct experiments with whole colonies of invasive species (possibly of varying sizes), allowing them to establish a territory that they can defend, although such an experimental protocol will be very labour intensive. A further limitation of the study is that the behavioural interactions were conducted in a small petri dish, which favoured a fast encounter of the two opponents and hindered escapes, possibly restricting the natural behaviour. In particular, species with evasive behaviour may have a lower mortality rate in the field (Spicer Rice and Silverman 2013b). Confrontation experiments with two species of *Formica* have shown that dominance behaviours may be contingent on many factors such as habitat type, resource value and competitor behaviour (Tanner and Adler 2009). Resource dispersion can also influence co-occurrence patterns (Lester et al. 2010). Further, group size can affect the behaviour and efficiency of different fighting strategies (Buczkowski and Bennett 2008a). For example, in interactions between *Li. humile* and the native *Tapinoma sessile*, the result depends on the group size in symmetrical interactions. Workers of *Li. humile* fight cooperatively and gain a local numerical advantage by attacking together (Buczkowski and Bennett 2008a). Similarly, soldiers may need recruitment to efficiently work together and give an advantage to *Ph. megacephala*. Future studies might test the effect of group size on the efficiency of different fighting strategies in invasive ants. Furthermore, in the field, different environmental conditions can favour different species and it has been suggested that the relative suitability can shift the dominance from one invasive species to another (Spicer Rice and Silverman 2013a). In that respect, temperature is especially important and different thermal preferences can be also a decisive factor determining the outcome of competition than interference performance (Cerdá et al. 1998; Wittman et al. 2010; Barbieri et al. 2015). The seasonal variation and the current state of the reproductive cycle can also influence the aggressiveness of a given colony (Tanner and Adler 2009 and references therein). In addition, the presence of disturbance can influence the dominance of invasive species (Foucaud et al. 2009). On Surprise island (South Pacific), different habitats were dominated by different ant species which won behavioural interactions at baits in 'their' habitat but not in others (Cerdá et al. 2012). Overall, mitigating biotic or abiotic factors have to be taken into account when making predictions for a particular community (Cerdá et al. 2013).

Generally, given similar life-history traits, ecological requirements and their aggressiveness against native species (Holway et al. 2002), the four highly aggressive species are likely to exclude each other (*W. auropunctata*, *La. neglectus*, *Li. humile*, *Ph. megacephala*). This is consistent with field observations of interactions between *Linepithema humile* and *Solenopsis invicta* (LeBrun et al. 2007), *Li. humile* and *Pheidole megacephala* (Lieberburg et al. 1975; Krushelnycky and Gillespie 2010) and *Li. humile* and *Pachycondyla chinensis* (Spicer Rice and Silverman 2013a). A possibility that cannot be discarded is that the three remaining species (*M. rubra*, *Pa. longicornis*, *A. gracilipes*) may co-exist with each other or even with one of the more aggressive species (Spicer Rice and Silverman 2013b). Co-existence of the 4 other species (*W. auropunctata*, *La. neglectus*, *Li. humile*, *Ph. megacephala*) or the clustering into local patches dominated by different species may happen, instead of a top dominant invasive species wiping out lower ranking species. One possible mechanism would be the existence of a discovery-dominance trade-off, where species excel either at discovering resources or dominating them but not both (Fellers 1987; Adler et al. 2007). There could also be a thermal tolerance-dominance trade-off, (Lessard et al. 2009; Arnan et al. 2012) as often observed in native communities (but see Santini et al. 2007; Parr and Gibb 2012). Similarly, thermophile native ants can co-exist with invasive ants (Thomas and Holway 2005). Whether such a trade-off exists among invasive ants remains to be investigated. In addition, species may occupy different micro-climatic niches allowing co-existence within the same area (Fluker and Beardsley 1970), while the macro-climatic conditions are predicted to be favourable for several species (Bertelsmeier et al. 2015). More field work is needed to assess co-existence patterns in a natural environment.

One intriguing question is how the two different interference strategies that we observed can produce similar impacts on native communities. One possibility is that the 'evasive' group (*M. rubra*, *Pa. longicornis*, *A. gracilipes*) does not display the same behaviour towards native species. Perhaps these species are evasive only when confronted with a very aggressive invasive species and more aggressive towards native species. This is the case in a native community where three dominant taxa (*Brachymyrmex*, *Solenopsis* and *Crematogaster*) frequently display aggressive behaviour towards a submissive species but never interact with each other (Bestelmeyer 2000). But this would imply that the 'evasive' species have some way of estimating the strength of their competitor (which is consistent with with one interpretation of our observed correlation between attack and success, Fig. 1). Another possibility is that the negative impacts of these species on native biodiversity are not so much due to direct interference as to resource exploitation or other indirect effects. For example, *A. gracilipes* is able to greatly alter community structure but only when it is very abundant and able to numerically dominate the food resource (Lester et al. 2009). This species has already been noted for its superior exploitation (discovery) and lower fighting abilities (Sarty et al. 2006).

A common observation for all seven invasive species was that their survival (*SI*) was systematically higher than their killing abilities (*KI*) and it would be interesting to know whether this corresponds to a general tendency in ants or whether this high survival rate is another key to their invasion success.

Our study illustrates the use of complementary dominance indices, demonstrating that the complexity of dominance relationships between different invasive species and their different behavioural strategies could not be captured by a single summary index (such as *SI*, *KI* or *DI*). If invasive ants have different behaviours and do not universally break the discovery-dominance trade-off, this can have consequences for management strategies. For example, it has been suggested that toxic baits have only minimal negative impacts on native ants because *Li. humile* is a faster discoverer of the baits and is able to dominate them (Buczkowski and Bennett 2008b). However, for invasive ants that do not show the same behaviour, toxic baits may have much greater impacts on non-target species. Gaining a better understanding of behavioural differences among invasive ant species will help to improve the understanding, prediction and management of invasions.

The surprising discovery of two different behavioural strategies among invasive ants could be relevant to how we view invasive species in general. Numerous studies attempt do define characteristics of invasive species for many different taxonomic groups, such as birds (Blackburn et al. 2009), plants (Pyšek et al. 2012) or fungi (Philibert et al. 2011). But searching for a quantitative trait difference between 'invasive' and 'non-invasive' species will give contradicting or non-significant results if species within the 'invasive' group display heterogeneous strategies.

Acknowledgments We would like to thank Phil Lester and two anonymous referees for their comments und suggestions on the manuscript, Jessica Purcell for language editing, Gloria Luque, Camille Leclerc, Cyrian Courchamp for their help in the lab, Sébastien Ollier for help with the statistical analyses. This paper was supported by Région Ile-de-France (03-2010/GV-DIM ASTREA), Agence Nationale de la Recherche (ANR, 2009 PEXT 010 01) and BiodivERsa Eranet grants. L.D. is funded by the FRIA (Fonds pour la Recherche dans l'Industrie et dans l'Agriculture) and a Newton International Fellowship. This work has also benefited from an Investissement d'Avenir grant managed by the Agence Nationale de la Recherche (CEBA, ANR-10-LABX-25-01).

References

Abril S, Gomez CG (2011) Aggressive behaviour of the two European Argentine ant supercolonies (Hymenoptera: Formicidae) towards displaced native ant species of the northeastern Iberian Peninsula. Myrmecol News 14:99–106

Adler F, LeBrun E, Feener D Jr (2007) Maintaining diversity in an ant community : modeling, extending, and testing the dominance-discovery trade-off. Am Nat 169:323–333

Arnan X, Cerdá X, Retana J (2012) Distinctive life traits and distribution along environmental gradients of dominant and subordinate Mediterranean ant species. Oecologia 170:489–500

Bacon SJ, Aebi A, Calanca P, Bacher S (2014) Quarantine arthropod invasions in Europe: the role of climate, hosts and propagule pressure. Divers Distrib 20:84–94

Bang A, Deshpande S, Sumana A, Gadagkar R (2010) Choosing an appropriate index to construct dominance hierarchies in animal societies: a comparison of three indices. Anim Behav 79:631–636

Barbieri RF, Grangier J, Lester PJ (2015) Synergistic effects of temperature, diet and colony size on the competitive ability of two ant species. Austral Ecol 40:90–99

Bertelsmeier C, Luque GM, Courchamp F (2013a) Increase in quantity and quality of suitable areas for invasive species as climate changes. Conserv Biol 27:1458–1467

Bertelsmeier C, Luque GM, Courchamp F (2013b) Global warming may freeze the invasion of big-headed ants. Biol Invasions 15:1561–1572

Bertelsmeier C, Luque GM, Hoffmann BD, Courchamp F (2015) Worldwide ant invasions under climate change. Biodivers Conserv 24:117–128

Bestelmeyer BT (2000) The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. J Anim Ecol 69:998–1009

Blackburn TM, Cassey P, Lockwood J (2009) The role of species traits in the establishment success of exotic birds. Glob Change Biol 15:2852–2860

Blight O, Provost E, Renucci M et al (2010) A native ant armed to limit the spread of the Argentine ant. Biol Invasions 12:3785–3793

Buczkowski G, Bennett GW (2008a) Aggressive interactions between the introduced Argentine ant, *Linepithema humile* and the native odorous house ant, *Tapinoma sessile*. Biol Invasions 10:1001–1010

Buczkowski G, Bennett GW (2008b) Detrimental effects of highly efficient interference competition: invasive argentine ants outcompete native ants at toxic baits. Environ Entomol 37:741–747

Carpintero S, Reyes-López J (2008) The role of competitive dominance in the invasive ability of the Argentine ant (*Linepithema humile*). Biol Invasions 10:25–35

Cerdá X, Retana J, Cros S (1997) Thermal disruption of transitive hierarchies in Mediterranean ant communities. J Anim Ecol 66:363–374

Cerdá X, Retana J, Manzaneda A (1998) The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. Oecologia 117:404–412

Cerdá X, Angulo E, Caut S, Courchamp F (2012) Ant community structure on a small Pacific island: only one native species living with the invaders. Biol Invasions 14:323–339

Cerdá X, Arnan X, Retana J (2013) Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology? Myrmecol News 18:131–147

Chazeau J, Potiaroa T, Bonnet de Larbogne L, Konghouleux J, Jourdan H (2000) La "fourmi électrique" *Wasmannia auropunctata* (Roger) en Nouvelle-Calédonie: expression de l'invasion, moyens d'une maîtrise de la nuisance en milieu agricole, praticabilité d'une préservation des milieux naturels. Convention Territoire de Nouvelle-Calédonie/IRD/1999. Conventions Sciences de la Vie, Zoologie Appliquée, IRD Nouméa, vol 10, pp 63

Dejean A, Moreau CS, Kenne M, Leponce M (2008) The raiding success of *Pheidole megacephala* on other ants in both its native and introduced ranges. CR Biol 331:631–635

Dussutour A, Simpson SJ (2008) Description of a simple synthetic diet for studying nutritional responses in ants. Insectes Soc 55:329–333

Errard C, Delabie JHC, Jourdan H, Hefetz A (2005) Intercontinental chemical variation in the invasive ant *Wasmannia auropunctata* (Hymenoptera: *Formicidae*) a key to the invasive success of a tramp species. Naturwissenschaften 92:319–323

Essl F, Dullinger S, Rabitsch W et al (2011) Socioeconomic legacy yields an invasion debt. Proc Natl Acad Sci USA 108:203–207

Fellers J (1987) Interference and exploitation in a guild of woodland ants. Ecology 68:1466–1478

Fitzpatrick MC, Weltzin JF, Sanders NJ, Dunn RR (2007) The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? Glob Ecol Biogeogr 16:24–33

Fluker S, Beardsley J (1970) Sympatric associations of three ants: *Iridomyrmex humilis*, *Pheidole megacephala* and *Anoplolepis longipes* in Hawaii. Ann Entomol Soc Am 63:1290–1296

Foucaud J, Orivel J, Fournier D et al (2009) Reproductive system, social organization, human disturbance and ecological dominance in native populations of the little fire ant, *Wasmannia auropunctata*. Mol Ecol 18:5059–5073

Hölldobler B, Lumsden CJ (1980) Territorial strategies in ants. Science 210:732–739

Holway DA (1998) Factors governing rate of invasion: a natural experiment using Argentine ants. Oecologia 115:206–212

Holway DA (1999) Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. Ecology 80:238–251

Holway DA, Lach L, Suarez AV et al (2002) The causes and consequences of ant invasions. Annu Rev Ecol Syst 33:181–233

Human KG, Gordon DM (1996) Exploitation and interference competition between the invasive Argentine ant, *I.linepithema humile*, and native ant species. Oecologia 105:405–412

IUCN SSC Invasive Species Specialist Group (2012) Global invasive species database. www.issg.org/database. Accessed 24 Jan 2014

Kabashima J, Greenberg L, Rust M, Paine T (2007) Aggressive interactions between *Solenopsis invicta* and *Linepithema humile* (Hymenoptera: Formicidae) under laboratory conditions. J Econ Entomol 100:148–154

Kirschenbaum R, Grace JK (2008) Agonistic responses of the tramp ants *Anoplolepis gracilipes*, *Pheidole megacephala*, *Linepithema humile*, and *Wasmannia auropunctata* (Hymenoptera : Formicidae). Sociobiology 51:673–683

Krushelnycky PD, Gillespie RG (2010) Correlates of vulnerability among arthropod species threatened by invasive ants. Biodivers Conserv 19:1971–1988

Lach L, Hooper-Bui LM (2010) Consequences of Ant Invasions. In: Lach L, Parr CL, Abbott KL (eds) Ant Ecol. Oxford University Press, Oxford, pp 261–286

Le Breton J (2003) Etude des interactions entre la fourmi *Wasmannia auropunctata* et la myrmécofaune: comparaison d'une situation en zone d'introduction: la Nouvelle-Calédonie et d'une situation en zone d'origine: la Guyane Française. Thèse de doctorat, Université Paul Sabatier, Toulouse 3; IRD, 233 p

Le Breton J, Orivel J, Chazeau J, Dejean A (2007) Unadapted behaviour of native, dominant ant species during the colonization of an aggressive, invasive ant. Ecol Res 22:107–114

LeBrun EG, Tillberg CV, Suarez AV et al (2007) An experimental study of competition between fire ants and Argentine ants in their native range. Ecology 88:63–75

Lessard J-PP, Dunn RR, Sanders NJ (2009) Temperature-mediated coexistence in temperate forest ant communities. Insectes Soc 56:149–156

Lester PJ, Abbott KL, Sarty M, Burns K (2009) Competitive assembly of South Pacific invasive ant communities. BMC Ecol 9:3

Lester PJ, Stringer LD, Haywood J (2010) The role of resource dispersion in promoting the co-occurrence of dominant and subordinate ant species. Oikos 119:659–668

Lieberburg I, Kranz P, Seip A (1975) Bermudian ants revisited: the status and interaction of *Pheidole Megacephala* and *Iridomyrmex Humilis*. Ecology 56:473–478

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species: a selection from the global invasive species database. Invasive Species Specialist Group, Auckland, p 12

Miravete V, Roura-Pascual N, Dunn RR, Gomez C (2014) How many and which ant species are being accidentally moved around the world? Biol Lett 10:20140518

Parr C, Gibb H (2012) The discovery-dominance trade-off is the exception rather than the rule. J Anim Ecol 81:233–241

Passera L (1994) Characteristics of tramp species. In: Williams D (ed) exotic ants: biology, impact, and control of introduced species. Westview Press, Boulder, CO, pp 23–43

Philibert A, Desprez-Loustau M-L, Fabre B et al (2011) Predicting invasion success of forest pathogenic fungi from species traits. J Appl Ecol 48:1381–1390

Pyšek P, Jarošík V, Hulme PE et al (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Glob Change Biol 18:1725–1737

Rabitsch W (2011) The hitchhiker's guide to alien ant invasions. Biocontrol 56:551–572

Roura-Pascual N, Brotons L, Peterson AT, Thuiller W (2009) Consensual predictions of potential distributional areas for invasive species: a case study of Argentine ants in the Iberian Peninsula. Biol Invasions 11:1017–1031

Rowles AD, O'Dowd DJ (2007) Interference competition by Argentine ants displaces native ants: implications for biotic resistance to invasion. Biol Invasions 9:73–85. doi:10.1007/s10530-006-9009-5

Sagata K, Lester PJ (2009) Behavioural plasticity associated with propagule size, resources, and the invasion success of the Argentine ant, *Linepithema humile*. J Appl Ecol 46:19–27

Santini G, Tucci L, Ottonetti L, Frizzi F (2007) Competition trade-offs in the organisation of a Mediterranean ant assemblage. Ecol Entomol 32:319–326

Sarty M, Abbott KL, Lester PJ (2006) Habitat complexity facilitates coexistence in a tropical ant community. Oecologia 149:465–473

Simberloff D, Martin J-L, Genovesi P et al (2013) Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol 28:58–66

Spicer Rice ES, Silverman J (2013a) Propagule pressure and climate contribute to the displacement of *Linepithema humile* by *Pachycondyla chinensis*. PLoS One 8:e56281

Spicer Rice ES, Silverman J (2013b) Submissive behaviour and habituation facilitate entry into habitat occupied by an invasive ant. Anim Behav 86:497–506

Suarez AV, McGlynn TP, Tsuitsui ND (2010) Biogeographic and taxonomic patterns of introduced ants. In: Lach L, Parr CL, Abbott KL (eds) Ant Ecol. Oxford University Press, New York, pp 233–244

Tanner CJ, Adler FR (2009) To fight or not to fight: context-dependent interspecific aggression in competing ants. Anim Behav 77:297–305

Thomas ML, Holway DA (2005) Condition-specific competition between invasive Argentine ants and Australian Iridomyrmex. J Anim Ecol 74:532–542

Wittman SE (2014) Impacts of invasive ants on native ant communities (Hymenoptera: *Formicidae*). Mymecol News 19:111–123

Wittman SE, Sanders NJ, Ellison AM et al (2010) Species interactions and thermal constraints on ant community structure. Oikos 119:551–559