

Local co-occurrence of several highly invasive ants in their native range: are they all ecologically dominant species?

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Abstract An important goal of invasion ecology is to understand the colonization, establishment, and spread of exotic species. To accomplish this, it is essential to examine the ecology of introduced species in native populations. We examined organization patterns, spatial structure, and competitive abilities of ground-dwelling ants in different habitats of a protected area in east-central Argentina, where several highly invasive ant species naturally coexist, to determine whether all they are ecologically dominant in their native range as in their introduced range. We sampled ant communities at Otamendi Nature Reserve and found 49 ant species co-occurred with moderate separation among habitats, including five species that are global invaders; but only *Solenopsis richteri* (the most numerically dominant) and *Linepithema humile* (the best mass recruiter) were ecologically co-dominant along with another three non-invasive species in locally rich assemblages. Their co-occurrence was apparently facilitated by both niche and competitive differences. However, we found no evidence for discovery-dominance trade-offs, and ant diversity and spatial segregation suggested that competition only plays a secondary role in structuring assemblages in arboreal habitats. Despite *L. humile* and *S. richteri* were ecologically co-dominant, their hegemony was lower in the reserve than in their introduced range likely due to biotic resistance. The other invasive ants (*Wasmannia auropunctata*, *Brachymyrmex patagonicus*, and *Nylanderia fulva*) were not dominant. It is possible that their establishment, persistence,

and high prevalence in anthropic habitats in native and introduced populations to be attributed to their better physiologic adaptations to disturbed habitats rather than to their superior competitive abilities.

Keywords Competitive mechanisms · Local assemblages · Biological invasions · Spatial partitioning · Habitat fidelity

Introduction

Widespread invasive species are considered a threat to biodiversity, homogenizing the world's biota by replacing and/or reducing native species (Vitousek et al. 1996; Simberloff 1997). Given the enormous ecological problems and economic costs associated with biological invasions (Pimentel et al. 2000), it is necessary to understand the factors influencing colonization, establishment, spread, and impact of introduced species (Elton 1958; Hutchinson 1959). An important step to achieve this is to understand the ecology of, for example, highly invasive ant species in their native ranges (Holway and Suarez 1999; Parr and Gibbs 2010; Foucaud et al. 2013).

More than 250 ant species have been reported as introduced into exotic ranges, but the actual number might be up to three times larger (Suarez et al. 2010). Although only a small number of introduced ant species cause ecological or economic damage, they are responsible for the loss of diversity of ants and other arthropods in many invaded regions (Holway et al. 2002). Many introduced ants share characteristics related with invasiveness: polygyny (multiple queens); unicoloniality, with multiple interconnected nests; reproduction by budding (a new colony is formed from a split of a mature colony); adaptation to anthropic habitats (e.g.,

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higher desiccation and thermal tolerance); and easy global dispersion by commerce (Hölldobler and Wilson 1990).

The knowledge of sources of invasive species is essential to prevent future introductions and/or to improve the management of current invaders. Three of the most damaging invasive species, the Argentine ant, *Linepithema humile*, the red imported fire ant, *Solenopsis invicta*, and the little fire ant, *Wasmannia auropunctata* (Lowe et al. 2000), are from South America (McGlynn 1999; Suarez et al. 2010). Recent molecular studies revealed that introduced populations of most of these species could have originated in naturally disturbed habitats, such the Paraná and Paraguay River floodplains, where they are very abundant (Tsutsui et al. 2001; Vogel et al. 2010; Asuncion et al. 2011; Rey et al. 2012).

Effects of climate on the physiology of invasive species are the second barrier in the process of invasion after the geographical barrier (Hellmann et al. 2008). Physiological limitations and secondarily competition, predation, and diseases are other important biotic factors influencing the possibilities of establishment and expansion in invasive species (Suarez et al. 2005; Lockwood et al. 2007). Rich ant communities with highly competitive species, and other natural enemies may be especially resistant to invasion by exotic ant species (Walters and Mackay 2005; Krushelnicky et al. 2010; Helford 2012).

Interspecific competition is thought to be a key factor structuring local ant communities (Hölldobler and Wilson 1990). Many ant assemblages are organized into dominance hierarchies based on differences in aggressiveness among species at food sources (Cerdá et al. 2013). The most aggressive species occupy the top of the dominance hierarchy, whereas the non-aggressive (submissive) subordinate species rank in the bottom (Savolainen and Vepsäläinen 1988). However, the fast discovery and consumption of resources before others (exploitation competition) allows behaviorally subordinate species to coexist successfully with dominant species that have the ability to secure resources either directly by aggression, or indirectly by maintaining a territory (Fellers 1987; Davidson 1998).

The trade-off between the abilities to discover and dominate a resource has been considered a key factor promoting the coexistence of ant species in the community (Fellers 1987; Kneitel and Chase 2004; LeBrun and Feener 2007). However, such trade-off seems to be more the exception rather than the rule in ant communities (Parr and Gibb 2012). Other interrelated factors, such as the dominance-thermal tolerance trade-off and niche differentiation (nesting requirements, foraging times, and diet), or stochastic processes mostly related to colonization, appear to be more relevant to promote species coexistence (Hubbell 2001; Delsinne et al. 2007; Tillberg et al. 2007; Andersen 2008; Mayfield and Levine 2010; Gibb and Parr 2010; Cerdá et al. 2013; Andersen et al. 2013; Stuble et al. 2013).

General analysis of the organization of the local ant assemblages in their native range can help to understand why some species become successful invaders. Unfortunately, most studies of invasive ants have focused on introduced populations. Little is known about organization patterns of ant assemblages in their native range in South America, where several species, invasive in a number of regions of the world, show regionally and/or locally overlapping distribution ranges. Only a few studies have focused on these species at the community level (e.g., Suarez et al. 1999; Folgarait et al. 2004; LeBrun et al. 2007; Tillberg et al. 2007; Calcaterra et al. 2008; Feener et al. 2008).

The Otamendi Natural Reserve (ONR) is a protected area located in the northeast of the province of Buenos Aires, on the mouth of the Paraná River, 55 km NW of the city of Buenos Aires. The first ant species inventory of the ONR was reported by Fuentes et al. (1998) with a descriptive study of the assemblages, which included three highly invasive ant species (the black fire ant *Solenopsis richteri* Forel, *L. humile*, and *W. auropunctata*), but without examining the interactions between the species. Most *L. humile* introductions around the world have been originated from source populations in or close to the ONR (Vogel et al. 2010), though others have been likely originated from near the port city of Rosario (Tsutsui et al. 2001). The recent discovery of a population of *W. auropunctata* from Zárate (only 15 km NW from the ONR) as the source population of the little fire ant introduction in Israel (Rey et al. 2012; Chifflet et al. 2016) also supports the idea that this region next to the transoceanic ports of Buenos Aires and Rosario is one of the main sources of invaders around the world.

The main objectives of this study were to characterize the ant community structure to study co-occurrence patterns, and to investigate the discovery, recruitment, and dominance abilities of the most common ant species in the ONR, with particular attention on *L. humile*, *W. auropunctata*, and *S. richteri*. The ultimate goal was to answer the following questions: (1) Are invasive ant species also ecologically dominant in their native range? If so, (2) what are the main factors determining their dominance in local assemblages? If not, (3) are ant communities governed by other dominant species or competition plays a secondary role in structuring local ant assemblages, even where a number of globally significant invasive ants occur?

Materials and methods

Study area

The study was conducted at the ONR (34°13'S, 58°54'W) from March 2007 to April 2008; sampling efforts were concentrated during the warmer months (Nov–Apr) when

ants were more active. The 3000 ha of the ONR have a marked topographic gradient including four major contiguous habitats (APN 2008): (1) Wetlands (“Pajonal”), located in the alluvial plains of the Paraná River and occupying 85 % of the ONR, with a mixture of scrubland, grasses, and other vegetation adapted to periodic flooding; (2) Pampean grasslands (“Pastizal”) located in the uplands, composed of grasses and forbs and occupying 4 % of the ONR; (3) Shrubland (“Chilcal”), also located in the uplands, mainly of the shrub *Baccharis salicifolia* and some grasses, and comprising 2 % of surface of the reserve; and (4) Forest (“Talar”), located on the edge of the scarp riparian corridor of the Paraná River, originally dominated by *Celtis tala* trees, but now invaded by exotic trees like *Ligustrum lucidum*, *Morus alba*, and *Melia azedarach*, covering only 0.8 % of the reserve. The rest of the surface is occupied by gallery forest habitat on the margins of the Parana River (3.4 %), and open water bodies (4.5 %). The uplands show moderate anthropomorphic disturbance, while the floodplains are less modified but undergo natural disturbance (stress) by frequent flooding.

Ant survey

A combination of pitfall traps and baits (Savolainen and Vepsäläinen 1988; King and Porter 2005; Calcatera et al. 2008) were used to study the ant fauna in the four habitats of the ONR.

Pitfall traps

Pitfall traps consisted of 50 mL plastic tubes (~3 cm diameter) buried in the ground and half-filled with soapy water. A total of 400 traps were placed along 40 linear transects (sampling units) located in homogeneous patches of vegetation. Transects of 45 m long were always separated at least by 50 m to ensure independence of samples and were distributed as follows: 12 in the grassland, 10 in the shrubland, 12 in the forest, and 9 in the wetland, covering a total sampled surface of ~7 ha. Unfortunately, three transects from the wetland were lost because pitfall traps were inundated by Paraná River floods and intense rains, remaining only six transects. Ten pitfall traps were set up every 5 m along the linear transects and exposed for 48 h.

Bait traps

A total of 290 baits were distributed in 29 of the above transects (ten baits per transect) to record the occurrence of ant species, the number of recruited ants, and interspecific interactions at baits, as follows: 9 transects in the grassland, 7 in the shrubland, 8 in the forest, and 5 in the wetland. The baits were exposed for 90 min at different times of day

between 9 a.m. and 18 p.m. at the same locations of the pitfall traps; to avoid sampling interference, the bait trapping was conducted 2 days before or after the pitfall trapping.

Two types of baits were used to evaluate different abilities of the species to control food resources: (1) resources that must be consumed and defended in situ (~1 g of commercially canned tuna in oil) and (2) resources that can be individual (e.g., *Ectatomma*) or collectively (e.g., *Pheidole* spp.) transported and consumed later inside the nest, a house cricket, *Acheta domesticus* (~0.7 g in average), as in LeBrun (2005) and Calcatera et al. (2008). Baits were placed alternately in the center of 5 cm diameter plastic cards along transects. The presence of phorid flies (Phoridae) chasing workers at baits was also recorded to document potential interference with ant activities.

Temperature and humidity were taken with a portable weather station at 1.5 m above the ground during baiting experiments between November 2007 and April 2008. Measures were taken at the start and end (90 min) of each baiting sampling. Overall mean (\pm SD) temperature and relative humidity (grouping all measures) was 28.3 ± 3.9 °C (range 23.2–35 °C) and 56.9 ± 11.9 % (range 36–86 %), respectively. Historical mean annual rainfall is ~950 mm (Cabrera and Willink 1980).

Representative individuals of each putative species attracted to the baits were collected and preserved in 96 % alcohol for identification to species or morphospecies using available keys. Voucher specimens were deposited in the entomological collections of the Instituto y Fundación Miguel Lillo (IFMM), Tucumán, Argentina and the Fundación para el Estudio de Especies Invasivas (FuEDEI), Buenos Aires, Argentina.

Species diversity

The number of ant species was recorded at the transect level (ten pooled pitfall traps), at the habitat level (pooling transects), and grouping all habitats (entire reserve level). Mean species richness was compared among habitats with transect as sampling unit using a generalized linear model (GLM) with Poisson distribution and log-link function corrected for overdispersion in STATISTICA v. 7.1 (StatSoft 2005). Abundance was measured by (1) the frequency of occurrence (proportion of traps and transects) with each species (spatial dominance or prevalence = SD) and (2) relative percentage of workers of each species captured in pooled pitfall traps (numerical dominance = ND) for each habitat and for the entire reserve (King and Porter 2005; LeBrun et al. 2007; Calcatera et al. 2008).

Species richness as a function of the sampling effort was analyzed using presence–absence data at the transect level (ten pooled pitfall traps) with EstimateS 9.1 software

(Colwell 2000). The observed number of species was then compared with the expected number of species (as calculated by the non-parametric first-order Jackknife richness estimator) as a tool to evaluate sampling efficacy (or inventory completeness).

Species composition

A two-dimensional ordination of samples was conducted with non-metric multidimensional scaling (NMDS) by using the Sørensen distance measure on presence–absence data to visually compare similarity patterns among transects (sampling unit) of each habitat as determined by the composition of their ant assemblages. The ordination was performed using Pc-Ord 4.0 (McCune and Mefford 1999) and tested using a nonparametric multivariate Analysis of Similarity (ANOSIM based on 1000 permutations and post hoc Bonferroni pairwise comparisons performed using past version 1.17 (Hammer et al. 2001).

An analysis of indicator species was carried out using the indicator value method (Dufrene and Legendre 1997) to determine which species were more abundant and frequent within each habitat. This method identifies the characteristic species for the habitat with the index IndVal. The index quantifies the fidelity and specificity of species in relation to groups of samples from different habitats. IndVal reaches its maximum (100) when all individuals of a species are found in a single habitat type and when the species occurs in all transects of that habitat. The significance of the maximum indicator value for each species was evaluated using a Monte Carlo randomization test (1000 iterations, significance level = 0.05). Only species present in >20 % of the samples were analyzed. The analyses were performed using Pc-Ord 4.0; this software permits the analysis of multivariate unbalanced ecological data.

Discovery, recruitment, and dominance

The first species approaching and staying on the baits for at least 5 s was considered the discoverer. If two species arrived together, both of them were considered the discoverers. The relative ability of the five most common species at baits (representing 73 and 80 % of all baits discovered and dominated, respectively) to discover the baits was quantified by the residual method (LeBrun and Feener 2007). The degree in which a species departed from its expected discovery value (null model) is defined as the residual discovery (RD) and measures the discovery ability of the species independent of their abundance in the environment. The null model consisted of the total number of baits discovered by the five more common species divided by the total number of times each of these species was recorded in a pitfall trap. This proportion was multiplied by

the number of pitfall traps each species was present into generate the expected number of baits that species would discover if all species were equally good discoverers (for more details see LeBrun and Feener 2007; Calcaterra et al. 2008; Feener et al. 2008). RD values were correlated with the proportion of traps where a species was present and it was the discoverer of the bait (FD).

Once baits were discovered, the recruitment response was recorded every 15 for 90 min. Recruitment patterns of the four most abundant species captured in pitfall traps and baited at the ONR were compared using a generalized linear mixed model (GLMM) analysis, with “species” as a fixed factor with four levels, “time” as a random factor with six levels, a Poisson distribution and a log-link function. Analyses were conducted using the glmer function in the lme4 package of R statistical software, version 2.4 (<http://www.r-project.org>). Only baits in which only one species attended were used for this analysis. Thus, recruitment curves were constructed for the four species with the highest number of replicates that allowed an adequate statistical analysis.

After 90 min, the proportion of baits dominated by each species either behaviorally (via aggressive contests to defend the bait in situ or its individual or collective transport into the nest) and/or numerically (recruiting a number greater of workers) was recorded. As in Morrison et al. (2000) and Calcaterra et al. (2008), a species dominated a bait when at least five workers were recruited and stayed in the bait for at least 30 min, with no more than two workers of other species being present. An attempt to usurp a bait occurred when at least three workers of a second species occupied the same station for at least 30 min. Turnover were those cases in which an usurper species displaced another species that was dominating a bait and retained it until the end of the observation period (90 min), recruiting at least five workers. These species and those that were able to defend the baits were considered the winners of the interactions.

Unfortunately, a behavioral-dominance hierarchy could not be constructed because of the scarce number of interactions between species observed at baits. Thus, the relationship between discovery and dominance was estimated by comparing the discovery and dominance scores for the nine species most frequently (conspicuous) occurring at baits (both dominant and subordinate species). For that, the number of baits discovered and dominated by each species was divided by their spatial abundance (or prevalence as measured by the number of pitfalls the species fell into) to provide a measure of relative discovery and dominance ability independent of their relative abundance (Parr and Gibbs 2012). A Chi-square test was used to test differences in the number of discovered and dominated baits by the five most dominant species and to evaluate if abilities were affected by the type of bait used.

Ecological dominance [ED, defined by Davidson (1998), as the ability to control a food resource by the combination of behavioral and numerical dominance] was calculated as the number of baits dominated by a given species divided by the number of pitfall traps where that species was present, as in LeBrun et al. (2007) and Calcaterra et al. (2008). An ecologically dominant species has greater representation at baits than would be expected only from its numerical abundance in the area (Cerdá et al. 2013).

Spatial partitioning

Null model analyses (Gotelli and McCabe 2002) were used to test for non-random co-occurrence of species using the array of presence–absence data from pitfall traps with Ecosim version 7.0 (Gotelli and Entsminger 2006). Four analyses were performed for each habitat, using either (1) the whole ant assemblages, (2) only the most frequently occurring species in pitfall traps (>10 % traps occupied), (3) the most dominant species at baits (>25 % baits monopolized), or (4) only the invasive species. The C-score statistic was used as measure of co-occurrence (Stone and Roberts 1990). If the statistic is significantly greater than that obtained after 5000 randomly constructed assemblages using a fixed–fixed algorithm, then species coexisted less than expected by chance (segregation). This indicates that the assemblage is structured by competition. If both indices are statistically similar, the assemblage is considered to be randomly distributed, and if the observed index is statistically lower than that expected by random, species spatially overlapped more than expected by chance (aggregation).

Results

Forty-nine epigeous ant species were found in the four habitats sampled, including five species that are invasive in other regions of the world: *S. richteri*, *L. humile*, and *W. auropunctata*, and the tawny crazy ant, *Nylanderia fulva*, and the dark rover ant, *Brachymyrmex patagonicus*, which are reported for the first time for this protected area.

Species diversity

A total of 3052 workers of 49 ant species in 17 genera and 5 subfamilies were pitfall-trapped. Of them, the 17 species listed in Table 1 were captured in more than 25 % of the 40 transects, representing 87 % of total workers captured; six of them occurred in all habitats. *Pheidole cordiceps* and *Pheidole guilelmimuelleri* were the most widely distributed species, being captured in 60 % of transects, whereas *S. richteri* was the most abundant species with 509 workers, 16.7 % of all workers captured. The most abundant and

widely distributed species in particular habitats were *L. humile* in the grassland, *P. guilelmimuelleri* in the shrubland, *P. cordiceps* in the forest, and *S. richteri* in the wetland (Table 1).

The number of species captured in pitfall traps ranged from 31 in the grassland to 16 in the wetland (Table 2). The total observed richness (49 species) represented 79 % of the total number of expected species (62); the percentages were relatively similar in all habitats (71–80 %), which indicates that most species occurring in each habitat were captured. Expected values for the individual habitats ranged from 39.3 in the grassland to 22.7 in the wetland. Although the wetland seems to host a lower number of species than other habitats, mean richness of species was only marginally different among habitats (GLM: Wald $X^2 = 7.324$, $df = 3$, $p = 0.06$). All habitats also showed similar number of rare species, but more exclusive species occurred in the forest (Table 2).

Species composition

The ordination of the samples showed a marked variation in community composition among habitats, which was statistically significant for all paired comparisons (Fig. 1; ANOSIM: $R = 0.47$, $p < 0.001$). However, only nine species showed a significant association with a particular habitat: *B. patagonicus* (indicator value of 66.2 %, $p = 0.001$), and *Crematogaster quadriformis* (34.6 %, $p = 0.037$) with the grassland; *Ectatomma edentatum* (49.1 %, $p = 0.001$) and *W. auropunctata* (35.4 %, $p = 0.044$) with the shrubland; *P. cordiceps* (44.8 %, $p = 0.002$), *Pheidole aberrans* (43 %, $p = 0.008$; probably misidentified as *Pheidole taurus* by Fuentes et al. (1998)), *N. fulva* (39.7 %, $p = 0.017$), and the leaf-cutting ant *Acromyrmex lundii* (36.5 %, $p = 0.022$) with the forest; and *S. richteri* (40.8 %, $p = 0.012$) with the wetland.

Discovery, recruitment, and dominance

Of the 49 species collected in pitfall traps, 19 were also recorded at baits (the 12 most common are shown in Table 1): 12 species in the grassland, 11 in both the shrubland and the forest, and only five species in the wetland. The species most frequently attending baits were *P. guilelmimuelleri*, *S. richteri*, *L. humile*, *C. quadriformis*, and *P. cordiceps* (Table 3). *Pheidole guilelmimuelleri* was the best discoverer (RD 14.1), followed by *C. quadriformis* (2.3). The four best discoverers with >10 % of discovered baits were also frequently collected in pitfall traps. Residual discovery values for these species were strongly correlated with the proportion of pitfall traps where those species were present and where they were the discoverer of the bait (FD) (Table 3; Spearman rank correlation, $r_s = 1$, $p < 0.0000$).

Table 1 Most abundant ant species (>25 % of sampling units) captured using pitfall traps in the four habitats sampled in the Otamendi Natural Reserve

Species	No. workers captured (% of sampling units)									
	Grassland		Shrubland		Forest		Wetland		Total	
	<i>n</i> = 12		<i>n</i> = 10		<i>n</i> = 12		<i>n</i> = 6		<i>n</i> = 40	
<i>Solenopsis richteri</i> ^b	78	(50) ^a	43	(20) ^a	10	(17)	378	(83) ^a	509	(38)
<i>Pheidole cordiceps</i>	5	(17)	63	(90) ^a	321	(100) ^a	1	(17)	390	(60)
<i>Pheidole guilelmimuelleri</i>	78	(67) ^a	162	(70) ^a	52	(42) ^a	26	(67) ^a	318	(60)
<i>Linepithema humile</i> ^b	191	(67) ^a	103	(80) ^a	8	(25) ^a	2	(33)	304	(53)
<i>Pheidole aberrans</i>	17	(17)	12	(20)	148	(67) ^a	0		177	(30)
<i>Nylanderia fulva</i> ^b	12	(42)	50	(50) ^a	99	(83) ^a	0		161	(50)
<i>Solenopsis substituta</i>	43	(58) ^a	77	(60) ^a	22	(42)	0		142	(45)
<i>Pheidole radoszkowskii</i>	17	(50)	38	(30) ^a	69	(33) ^a	0		124	(33)
<i>Pheidole</i> sp. 1	17	(33)	22	(40)	46	(67)	0		85	(40)
<i>Pheidole bergi</i>	21	(17) ^a	9	(40)	45	(58) ^a	17	(17) ^a	92	(35)
<i>Pheidole</i> sp. 2	8	(25)	42	(50)	0		13	(33)	63	(25)
<i>Pheidole</i> sp. 3	27	(25)	10	(50)	24	(33)	0		61	(30)
<i>Crematogaster quadriformis</i>	36	(58) ^a	18	(40) ^a	0		0		54	(28)
<i>Ectatoma edentatum</i>	12	(42) ^a	26	(90) ^a	11	(33) ^a	0		49	(45)
<i>Wasmannia auropunctata</i> ^b	1	(8)	38	(60) ^a	2	(8)	1	(17)	42	(25)
<i>Acromyrmex lundii</i> ^c	2	(8)	7	(1)	14	(58)	2	(17)	25	(25)
<i>Brachymyrmex patagonicus</i> ^b	18	(75)	2	(10)	0		0		20	(25)
Other (32 species)	153		42		191		50		436	
Total worker no.	736		764		1062		490		3052	

^a Twelve of the 19 species that were also recorded at baits located at each habitat

^b Native ant species that has invaded other regions of the world

^c Native ant species considered a pest

Table 2 Diversity estimators in the four habitats sampled in the Otamendi Natural Reserve

No.	Grassland	Shrubland	Forest	Wetland	Total
Expected species ^a	39.3	36	36.3	22.7	61.7
Observed species (% of expected)	31 (79 %)	27 (75 %)	29 (80 %)	16 (71 %)	49 (79 %)
Mean species/sampling unit ± SE	8.6 ± 1.1a	9.4 ± 1.1a	9.1 ± 1.2a	4.6 ± 0.9a	8.37 ± 0.6
Exclusive species ^b	4	3	7	2	–
Rare species ^c	9	10	8	8	14

Lowercase letters within columns indicate non-significant differences among habitats ($p > 0.05$)

^a Estimated richness value with the most stable estimator (Jack1)

^b Observed species in only one habitat

^c Observed species in only one sampling unit or transect (unique or singleton)

The Argentine ant, *L. humile*, showed the highest recruitment rate with a mean number of 68.3 workers (maximum of 200) (Fig. 2). This pattern of recruitment was significantly different from patterns observed for other species (Table 3; GLMM: $Z = 16.37$, $p < 0.0000$). Despite being the least abundant, *C. quadriformis* showed the highest ecological dominance with 0.63, followed by *P. guilelmimuelleri* with 0.52, and *S. richteri* with 0.50

(Table 3). No differences were found in the number of discovered and dominated baits using tuna or crickets ($p > 0.05$).

The presence of parasitoid flies chasing ants at the baits was observed in 23 (11 %) of the 217 baits, as follows: *P. guilelmimuelleri* (9 baits), *Pheidole bergi* (7), *P. cordyceps* (2), *S. richteri* (2), *C. quadriformis* (1), *L. humile* (1), and *S. substituta* (1). The identification at the family level of some

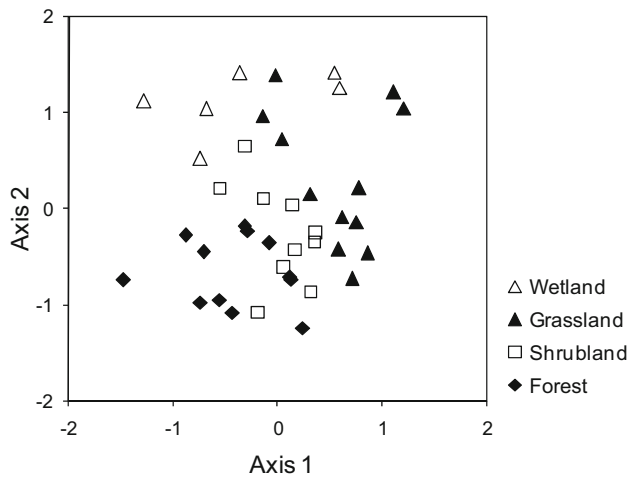


Fig. 1 Non-metric multidimensional scaling ordination plot from pitfall trap data showing differences in the species composition among sampling units (*points* represent transects) located in the four different habitats ($R^2 = 0.76$, stress 0.21). Only the 17 most common species were considered in the analysis (species present in more than 25 % of the samples)

flies collected at the end of the monitoring revealed that all were Phoridae; those attacking *S. richteri* were *Pseudacteon obtusus*.

Evidence of discovery-dominance trade-offs were not detected among directly competing species of the ant assemblages. In contrast, a strong positive relationship was found between discovery score and dominance score for the nine most conspicuous species at baits ($r_s = 0.92$, $p < 0.0005$, pooling the four habitats, Fig. 3). All but one species, *L. humile*, dominated fewer baits than those discovered, mostly in the grassland and the shrubland, but only *P. guilelmimuelleri* did so statistically significantly ($X^2 = 4.55$, $df = 1$, $p = 0.033$; Fig. 4). A similar positive relationship was observed in each individual habitat ($r_s = 0.75$ – 0.89 , $p < 0.05$), except in the wetland ($r_s = 0.7$, $p = 0.19$). Of the four species that dominated most baits (>15 %), *P. cordiceps* discovered and dominated fewer

baits than expected according to their relative occurrence in traps ($X^2 = 7.5$, $df = 1$, $p = 0.006$ and $X^2 = 7.9$, $df = 1$, $p = 0.004$, respectively; Fig. 4).

Spatial partitioning

A single species was captured in 29 % (118/400) of the pitfall traps and up to 15 species were recorded in a single trap. In contrast, a single species was found at 64 % (139/217) of the baits, and up to five species were found at a single bait. However, null model analyses from pitfall traps revealed only weak evidence of spatial segregation in the ant assemblages, both overall and among the most frequent species or invasive species at particular habitats.

Co-occurrence analysis at the habitat level indicated that only the entire ant assemblages and the invasive species in the shrubland coexisted significantly less than expected by chance (C-score_{obs} = 35.507, C-score_{exp} = 34.455, $p < 0.0001$ and C-score_{obs} = 104.700, C-score_{exp} = 99.396, $p < 0.005$, respectively). Coexistence in the other three habitats was similar to the expected values ($p > 0.2$ in all cases). Using the analysis of the most frequent species (>10 % of all pitfall traps) per habitat, only ants of the forest co-occurred marginally less than expected by chance (C-score_{obs} = 205.500, C-score_{exp} = 199.409, $p = 0.051$; $p > 0.3$ in all other habitats). Dominant species at baits (>10 % of monopolized baits) when considered together, co-occurred randomly in all habitats ($p > 0.1$ in all cases).

Discussion

One of the main findings of this work is the high local co-occurrence of native ant species that are well-known global invaders. However, only the invasive *S. richteri* and *L. humile* were ecologically co-dominant species along with another three non-invasive ant species, *P. guilelmimuelleri*, *P. cordiceps*, and *C. quadriciformis* in species-rich

Table 3 Discovery, recruitment, and dominance performance (relative ranking) of the five species most frequently at baits

Species	Discovery		MR	Dominance		
	FD	RD		SD	ND	ED
<i>P. guilelmimuelleri</i>	0.95 (1)	14.1 (1)	27.0 (2)	16.3 (3)	10.4 (3)	0.52 (2)
<i>S. richteri</i>	0.69 (3)	−0.6 (3)	20.7 (3)	14.5 (4)	16.7 (1)	0.50 (3)
<i>L. humile</i>	0.52 (4)	−20.1 (4)	68.3 (1)	18.8 (2)	10 (4)	0.35 (4)
<i>C. quadriciformis</i>	0.82 (2)	2.3 (2)	15.3 (5)	4.8 (5)	1.8 (5)	0.63 (1)
<i>P. cordiceps</i>	0.29 (5)	−32.6 (5)	16.8 (4)	21 (1)	12.8 (2)	0.21 (5)

^a *FD* (food discoverer): proportion of baits discovered first/occurrence in pitfall traps; *RD* (residual discovery): degree that a species departs from the expected discovery value; *MR* (mass recruitment): mean number of worker recruited during 90 min; *SD* (spatial dominance): proportion of traps in which a species was present; *ND* (numerical dominance): relative percentage of captured individuals of each species; *ED* (ecological dominance): proportion of baits dominated/occurrence in pitfall traps

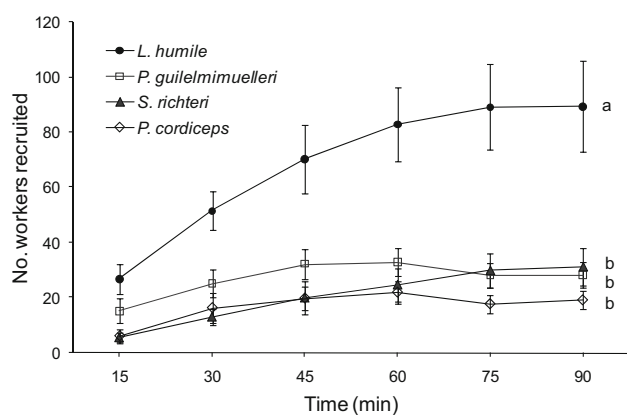


Fig. 2 Mean (\pm SE) number of workers recruited to the tuna baits (counted every 15 min) for the four most abundant species captured in pitfall traps and baited at the four surveyed habitats in the Otamendi Natural Reserve. The mean number of workers for each species was calculated considering all the baits in which at least one worker of that species was seen at the baits for all 90 min of observation. Sample sizes (baits) for each species are: *L. humile* (19), *P. guilelmimuelleri* (22), *S. richteri* (25), and *P. cordiceps* (22). Datalines with different letters are statistically significant ($p < 0.05$, GLMM)

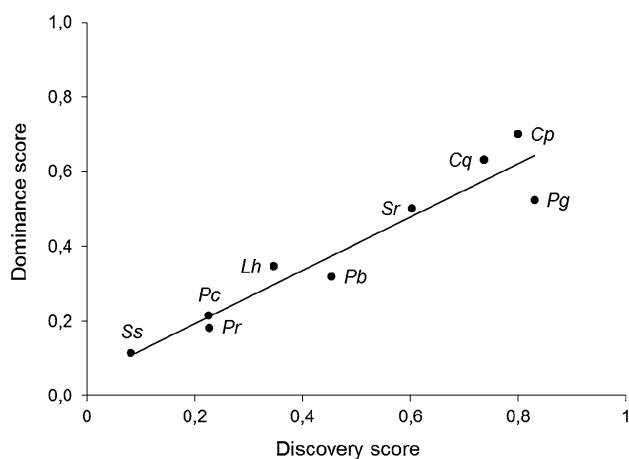


Fig. 3 Relationship between discovered and dominated baits for the nine most common ant species attracted to baits in the Otamendi Natural Reserve ($r_s = 0.92$, $p < 0.0005$): *Pg* = *Pheidole guilelmimuelleri*, *Sr* = *Solenopsis richteri*, *Lh* = *Linepithema humile*, *Pc* = *Pheidole cordiceps*, *Cq* = *Crematogaster quadriformis*, *Pb* = *Pheidole bergi*, *Cp* = *Camponotus punctulatus*, *Ss* = *Solenopsis substituta*, *Pr* = *Pheidole radoszkowskii*

assemblages. This is concordant with the observed in the case of the invasive fire ant (*S. invicta*), which was also ecologically co-dominant with *L. humile* and other non-invasive native ants in its native range (LeBrun et al. 2007; Calcaterra et al. 2008).

Ant coexistence in the ONR was influenced by the habitat type with moderate species separation among habitats, which agrees with the reported by Calcaterra et al. (2010) for ant communities the Iberá Natural Reserve in

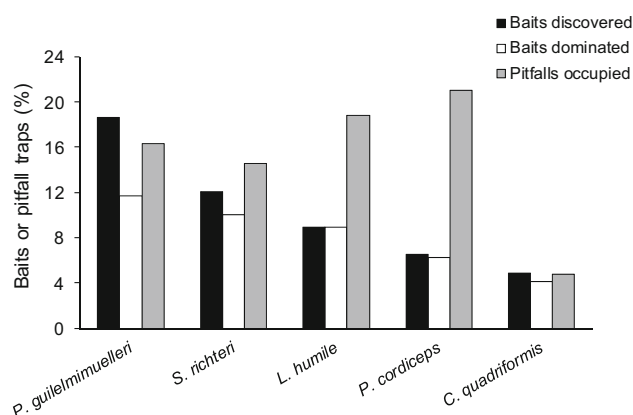


Fig. 4 Percentage of baits discovered, baits dominated, and pitfall traps occupied by the five most common ant species in the four habitats sampled in the Otamendi Natural Reserve ($n = 400$ pitfall traps and $n = 290$ baits)

northeastern Argentina. Most invasive species showed a strong fidelity to a particular habitat which facilitated their coexistence at the local scale. *Solenopsis richteri* was associated with the wetland, as in Fuentes (1999), being consistent with its adaptation to periodic flooding and the high insolation required for colony thermoregulation (Folgarait et al. 2004; Tschinkel 2006; Calcaterra et al. 2010; LeBrun et al. 2011). *Solenopsis richteri* was also the most common species observed by Folgarait et al. (2004) in low grasslands of the ONR susceptible to flooding.

The invasive *N. fulva* was associated with the forest, showing the highest vegetation complexity, the lowest insolation, and scarce litter coverage. Curiously, the highest number of exclusive species occurred in the forest. *Wasmannia auropunctata* was associated with the shrubland, the habitat with the highest litter coverage, while *B. patagonicus* was associated with the grassland. However, both species were associated with shrubland in Cerrado (savanna) biome in Brazil (Brandão et al. 2011). The Argentine ant was the only invasive species that not showing a clear preference for a particular habitat, likely because it was very abundant both in grassland and shrubland.

Linepithema humile, *S. richteri* and other co-dominant species in their native range also differed in their discovery, recruitment, and dominance performances likely facilitating also their local coexistence (Fellers 1987; Kneitel and Chase 2004; LeBrun and Feener 2007; Mayfield and Levine 2010). *Pheidole guilelmimuelleri* was the best discoverer and the second most ecologically dominant species being very prevalent and dominant in all habitats; although curiously it had been reported only for Misiones, in Argentina (Cuezco 1998). Moreover, *P. cordiceps* was spatially and numerically dominant in arboreal habitats, especially in the forest. However, it was not ecologically very dominant, presumably because of its poor performance as food source

discoverer and worker recruiter; it was observed monopolizing crickets (and plastic card with tuna) by cooperatively transporting them to the nests, as other invasive ant, *Pheidole obscurithorax* (Calcaterra et al. 2008), thus limiting the time for other ants to find and exploit that resource. *Pheidole cordiceps* was reported for several provinces of Argentina mainly distributed within Monte desert ecosystem (Cuezzo 1998). Unfortunately, nothing is known about the ecology of these two *Pheidole* species; they did not interact sufficiently with other dominant species at baits to establish their behavioral abilities to monopolize resources; consequently, their potential as invaders remains uncertain.

The low performance of *S. richteri* in finding resources and recruiting workers might be compensated by its aggressive behavior and high reproductive rate; because of this, it was the most numerically dominant species despite being less frequent than *P. cordiceps*, *L. humile*, and *P. guillelmuelleri*. The low ecological dominance of *S. richteri* in the ONR (its native range) and the fact that this is only very common and abundant in the Buenos Aires province is consistent with its spread in the United States limited northern Alabama and Mississippi (Tschinkel 2006).

The invasive Argentine ant showed the highest recruitment rate, with a pattern similar to that observed by Calcaterra et al. (2008) in a subtropical gallery forest (27°S) in northeastern Argentina. However, as in Suarez et al. (1999) and Bertelsmeier et al. (2015a), this behavioral advantage did not translate into a high ecological dominance; it dominated a scarce number of baits (9 %) maybe because of its low ability to aggressively defend resources, as observed by Bertelsmeier et al. (2015a, b) in laboratory assays.

In the ONR, *L. humile* locally coexists with other ant species that are just as dominant, or more so, some even invasive, in rich assemblages, a pattern also observed in other regions within their native range (Calcaterra et al. 2008; Feener et al. 2008). This strongly contrasts with that observed in some regions of its introduced range, such as in California (Holway 1998, 1999) and the Mediterranean (Vogel et al. 2009), where the Argentine ant is usually the only numerically dominant ant monopolizing up to 76 % of the baits by a rapid recruitment of high numbers of workers (Suarez et al. 1999). Thus, our data support studies by Suarez et al. (1999); LeBrun et al. (2007); and Calcaterra et al. (2008) indicating that the Argentine ant is overall not the most dominant ant species in its native range.

The Argentine ant has much smaller colonies in its native range (e.g., 11 polygyne colonies over a 3-km transect with widths ranging from 1 to 515 m in the ONR, Vogel et al. 2009) than in its introduced range, where one colony can extend until 900 km as the Californian colony in the US (Suarez et al. 2008) or exceptionally until 6000 km as the

mega-colony present along the Mediterranean coast in Europe (Giraud et al. 2002). According to Vogel et al. (2009), this size difference might be the result of the ecological release from ant competitors as those observed in the ONR and in other assemblages of its native range rather than a loss in genetic diversity and a shift in social organization in the new habitat (Vogel et al. 2009). However, though Roura-Pascual et al. (2011) found evidences for biotic resistance by native assemblages in the introduced range of *L. humile*; climatic suitability and habitat modification (e.g., irrigated deserts) were the main reasons for the distribution of this global invader, which is strongly dependent on water availability (and the resultant moisture) for its survival, colony growth, and consequent competitive success (Holway et al. 2002; Roura-Pascual et al. 2011). This seems to be the case of Australia, where *L. humile* has a limited ability to penetrate into natural habitats dominated by *Iridomyrmex* species because these are better able to tolerate hot and dry conditions (Thomas and Holway 2005).

Creumatogaster quadriciformis was the most ecologically dominant species and the second best discoverer, but it was numerically less abundant, discovering and dominating only a few baits. This agrees with Delsinne et al. (2007), who found it only in 4.2 % of 450 baits exposed in the dry Chaco ecosystem of northeastern Paraguay; where curiously its foraging behavior changed with bait type, showing an extirpator behavior for carbohydrates and an opportunist behavior for proteins. Interestingly, a diet higher in carbohydrates has been related with an increase in aggressiveness in Argentine ants (Grover et al. 2007); *L. humile* is one of the most carnivorous ants in the ONR (Tillberg et al. 2007).

The reason for the low abundance of *C. quadriciformis* is unknown; however, it could be explained by a low reproductive rate and small resultant colonies. We found *C. quadriciformis* more ecologically dominant than reported for subtropical habitats by Calcaterra et al. (2008) in Corrientes and by LeBrun et al. (2007) in Santa Fe, suggesting its better performance in lower (colder) latitudes (temperate habitats). Despite being poorly represented in the different environments, its usual aggressive behavior defending food resources would allow it to dominate more baits than expected. Despite being the most ecologically dominant species in the ONR and common in most of the provinces of Argentina (Cuezzo 1998), its potential as invader is uncertain. So far, this species has not been reported outside its native range.

Nylanderia fulva and *B. patagonicus* showed similar performances, discovering more baits than finally dominated, mainly in arboreal habitats (shrubland and/or forest). Although *W. auropunctata* was in general a little more abundant than *B. patagonicus*, it only discovered and dominated one bait in the shrubland. According to Berman et al. (2013), *W. auropunctata* is an opportunist species with

a low capacity for behaviorally dominating resources in natural ant assemblages in New Caledonia. Its lower abundance in natural habitats of the ONR could be also related with the fact this species experimented a recent spread likely as a consequence of the global warming (until 1 °C), extending its distribution during the last 60 years from Entre Ríos (Kusnezov 1952) to Buenos Aires (Cuezzo et al. 2015; Chifflet et al. 2016).

Although *W. auropunctata* was behaviorally more dominant than *L. humile* in pairwise-species confrontations conducted in laboratory by Bertelsmeier et al. (2015a), in natural habitats it would be able to defend only nest territories due to its slower performance to scout and quickly recruit workers to food sources (Bertelsmeier et al. 2015b; L.A.C. unpublished data). It is able to monopolize a food resource only when a large number of workers are recruited to it (Achury et al. 2008; Vonshak et al. 2012). However, its success as invader seems to be more associated with its clonal reproduction system mostly observed in anthropic habitats, which would have favored (fixed) genotypes with higher thermal tolerance (Foucaud et al. 2009; Rey et al. 2012; Chifflet et al. 2016) rather than with a superior competitive ability (L.A.C. unpublished data). This species has a marked preference for secondary forest with intermediate conditions of humidity and canopy cover over primary forest (Orivel et al. 2009; L.A.C. pers. obser.). *Wasmannia auropunctata*, *N. fulva*, and *B. patagonicus*, typically “tramp ants”, are very common and dominant in anthropic habitats with low species richness (Quirán et al. 2004; MacGown et al. 2007; Cuezzo et al. 2015; Josens et al. 2014).

It is interesting to mention that a similar clonality system was also observed in the highly invasive longhorn crazy ant, *Paratrechina longicornis* (Pearcy et al. 2011), phylogenetically close to *N. fulva*. However, *N. fulva*, the most recently introduced species into southeastern United States from South America (putatively also from the Paraná basin, Gotzek et al. 2012), has also been observed displacing the dominant *S. invicta* and reducing species diversity in rich-species grassland ant assemblages (Hill 2013; LeBrun et al. 2013). Similarly, it has been found in its homeland winning most contests against *S. invicta* in absence of phorid flies in the Pantanal, one of the largest Brazilian wetlands (Feener et al. 2008).

Although the discovery-dominance trade-off has been proposed as the most common mechanism explaining the coexistence among ant species (Davidson 1998), this mechanism was not observed among the most common dominant and subordinate species at baits in the ONR. The lack of trade-off is consistent with Gotelli and McCabe (2002), Ribas and Schroederer (2002), Sanders et al. (2003), Badano et al. (2005), Ward and Beggs (2007), and Calcaterra et al. (2008). With the exception of Feener et al.

(2008), dominance-discovery trade-offs were only detected in ant assemblages where behavioral dominant species were strongly attacked by parasitoid flies (LeBrun 2005; Parr and Gibb 2012). In this study, except on *P. guilelmimuelleri*, the presence of phorid parasitoids attacking dominant species was relatively low, suggesting a weak effect, if any, on the outcome of the interactions among ant species.

On the contrary, a strong positive relationship was found in most cases (75.6 %) between discovery and dominance scores at baits. This tentative linear hierarchy of dominance (Fig. 3) revealed that discoverer species mostly dominated (numerically) the resources without mediating agonistic interactions. *Pheidole guilelmimuelleri* was the only species that discovered more baits than finally dominated, suggesting its weak aggressive (defense) behavior. This has been also reported for *P. obscurithorax* (also attacked by phorid flies) in assemblages dominated by *S. invicta* in south tropical Argentinean habitats (LeBrun et al. 2007; Calcaterra et al. 2008); *P. obscurithorax* might have been also introduced in the United States from the Paraná River basin (Wild and Suarez 2009; Wetterer et al. 2015).

Ant species at the ONR rarely interacted at baits, as observed by Fuentes (1999). Only a single species was present at the majority of the baits, suggesting that the foraging ranges did not overlap, maybe because species cannot physiologically tolerate a microhabitat or competitive exclusion (territoriality). These are the most common mechanisms to explain segregation patterns in ant communities (Levings and Traniello 1981; Adams 1994; Bestelmeyer 2000; Mayfield and Levine 2010; Gibb and Parr 2010). As expected by the mosaic theory (Levings and Traniello 1981; Adams 1994; Vandermeer et al. 2008; Arman et al. 2009) and despite we only sampled above-ground ants, we only found evidence of segregation from pitfall trap data in arboreal habitats when analyzing (1) the entire species array and the five invasive species in the shrubland (where the scarcest interspecific interactions occurred) and (2) the most frequent species in the forest (e.g., *P. cordiceps*, *P. aberrans*, and *N. fulva*). Thus, competition could be organizing ant assemblages only at two of four habitats (the most arboreal ones). It agrees with Parr (2008), who observed that competition was only relevant at one of the three savanna studied habitats in the Kruger National Park (South Africa), where high abundance of dominant species promoted competitive exclusion. However, it seems not to be our case because we did not find highly abundant species able to competitively reduce species diversity. Thus, these results agree with those from other areas of the world, indicating that competition plays a limited role in species coexistence (Andersen 2008; Andersen et al. 2013).

In summary, this study revealed that five highly invasive species coexisted locally in rich local assemblages, but only *S. richteri* and *L. humile* were ecologically co-dominant

along with another three non-invasive ant species. Overall co-occurrence among invasive and/or co-dominant species in the ONR was apparently facilitated by both niche and competitive differences, because they had different habitat fidelity and performance to discover, recruit, and dominant resources. Although we did not detect evidences for discovery-dominance trade-offs, ant diversity and spatial segregation patterns suggested only a potential low influence of competition in structuring ant assemblages only in the two arboreal habitats.

Despite *L. humile* and *S. richteri* were co-dominant in their homeland, their supremacy was lower than in their introduced range, likely because another two non-invasive species were more ecologically dominant; unfortunately their potential as invaders remains uncertain. The release of strong competitor ants might explain, at least in part, the higher dominance of these and other behavioral dominant invasive ants (e.g., *S. invicta* and likely *N. fulva*) in their introduced range. However, in other cases (e.g., *W. auropunctata* and likely *B. patagonicus*), dominance in their native and introduced range seems to be more associated with their high colonization capacity to harsh environments (mostly anthropic) rather than to their superior competitive abilities.

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