

Impact of human dwellings on the distribution of the exotic Argentine ant: a case study in the Doñana National Park, Spain

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Received 7 August 2002; received in revised form 8 January 2003; accepted 18 March 2003

Abstract

The invasive Argentine ant *Linepithema humile* was found in close perimeters to inhabited houses situated in various habitat types in Doñana National Park (Southern Spain). We suggest that the Argentine ant is found in these sites largely due to passive importation by man, but from there may have the potential to spread into surrounding favourable natural habitats. Ant species richness and diversity around houses was similar to that in natural habitats, except in the cases where the Argentine ant dominated, where a considerable lower ant species diversity and richness was observed. The species composition of ants in the immediate vicinity of houses was very different from that of the surrounding natural habitats, although the species composition between houses was very similar, regardless of the type of surrounding natural habitat. Ant species around houses were typically generalists, opportunists or open habitat specialists. Many of these species are considered dominant in that they are characterised by having large nests, aggressive behaviour and mass recruitment in response to attack. However, these species are displaced by the Argentine ant when introduced. Not all ant species show the same responses to invasions by the Argentine ant, and some species, such as *Cardiocondyla batesii*, *Oxyopomyrmex saulcyi* or *Cataglyphis floricola*, may be able to persist for a period following an invasion of the Argentine ant. These species are characterised by small nests and submissive behaviour, and may survive by avoiding conflict with the invasive species.

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Keywords: *Linepithema humile*; Invasion; Doñana National Park; Spain; Vegetation and human influence; Indigenous ants

1. Introduction

Which factors make some habitats susceptible to invasion by the Argentine ant *Linepithema humile* (Mayr, 1868) or other exotic species? A number of ecological characteristics have been associated with the susceptibility of communities to invasion by exotic species, including low species richness, the absence of predators and parasites, the presence of empty niches and the appearance of new niches due to habitat disturbance (Hölldobler and Wilson, 1990; Holway, 1998a; Majer, 1994; Suarez et al., 1998). The truth is that it is practi-

cally impossible to make generalisations about which communities are susceptible or resistant to biological invasions, since the constants in theoretical models are, in reality, variables that depend on the species composition of the community and on the invading species. Therefore, in principle at least, all communities can be invaded. For example, even if a habitat is species-rich and all available niches are occupied, an invading species may be able to establish itself if the biotic conditions are favourable and it is able to displace resident species (Newman, 1993).

However, the regions of the world where *L. humile* now occurs, mostly areas characterised by a Mediterranean climate (including Europe, the Americas, Australia and South Africa), seem to be particularly susceptible to biological invasions. Although these areas have quite different ant communities depending on zoogeographical

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distribution of species and other factors, they share in common large scale anthropogenic disturbances including urban and agricultural development, which has threatened many species with extinction (Macdonald et al., 1988; Tremper, 1976).

Many protected ‘natural’ habitats have become ‘islands’ surrounded by severely disturbed habitats, whose biological communities may differ in both species composition and abundance from surrounding habitat, leading to relatively small and isolated communities that may be particularly sensitive to changes brought about by the introduction of new species. In Doñana National Park (Huelva, southwestern Spain), an area well known for its conservation value and ecological vulnerability, the non-native Argentine ant has already been found in several sites within the Park. Previous observations have suggested that the Argentine ant was concentrated around visitors centres and staff houses. However, it is unknown to what extent the Argentine ant is a real problem in Doñana, whether it occupies areas away from human dwellings or to what degree it is affecting native ant communities.

The aims of this study were, firstly to determine the distribution of *L. humile* in the Doñana Biological Reserve and surrounding areas, and to identify factors associated with the presence of *L. humile*, with respect to human dwellings, vegetation and native ant fauna. Secondly, to assess the impact of the Argentine ant on native ant species.

2. Methods

2.1. The ants

Workers of this species are small, medium to dark brown ants, reaching 2–3 mm in length. Workers are extremely fast moving, often recruiting in high numbers. As a typical ‘tramp’ ant, *L. humile* easily disperses around the world through commerce and other human-assisted avenues. It generally thrives in, although is not limited to, disturbed or modified habitat such as agricultural land and urban environments. Argentine ants have a generalist diet that includes, nectar, insect, seeds, and honeydew secreted by homopterous (Suarez et al., 1998).

2.2. Study site

Doñana National Park is located on the southwest coast of the Iberian peninsula (provinces of Huelva and Seville, Spain) and covers an area of approximately 56,000 ha, which includes a large area of marshland at the mouths of the Guadalquivir and Guadiamar rivers (Fig. 1). The local climate is ‘sub-humid’ Mediterranean influenced by the Atlantic, and according to Gausse’s

(1968) classification, is included in the Mediterranean climatic region.

The vegetation largely consists of scrubland sparsely populated with large isolated cork oaks (*Quercus suber*) and patches of introduced pines (*Pinus pinea*). As a result of its rolling topography, a legacy of the sand dune origin of the region, and a shallow water table, the higher areas are characterised by xerophytic vegetation, whilst the lower damper areas are characterised by hygrophytic vegetation (Rodríguez, 1991).

Within the Park there are various human dwellings including wardens houses, visitor centres, and within the Biological Reserve there is the ‘Palacio de Doñana’, an old hunting residence which is now an administrative and research centre (see Fig. 1). Some of these buildings are known to be occupied by the Argentine ant. In this study, we examine the ant fauna around eight wardens houses and the visitors centre at La Rocina (Table 1). These environments usually consist of small dwellings and auxiliary buildings such as chicken coups and stables. The largest of these groups of buildings are centred around the ‘Palacio de Doñana’ (where the Chalet is found) and the visitors centre at La Rocina. Exotic, ornamental or garden plants can sometimes be found around these centres of human activity.

These human habitats can be found within all the main habitat types in the National Park (described later). The higher elevation areas of the Park contain xerophytic scrubland or ‘monte blanco’ dominated by the shrub *Halimium halimifolium*. Other abundant plant species in the *monte blanco* habitat include *Cistus libanotis*, *Lavandula stoechas* and *Thymus mastichina*. Dense monotypic pine plantations also occur in dry areas, and are characterised by a low productivity and a sparse understorey of *Rosmarinus officinalis*, *H. halimifolium* and *L. stoechas* amongst others. In areas close to the marsh with higher soil humidity, the xerophytic scrubland gives way to a transition scrubland habitat (transitional *monte blanco*) characterised by more diverse vegetation and abundant grassy clearings. The main plant species in this habitat include *Ulex* spp., *Erica* spp., *Armeria velutina*, *H. halimifolium*, *H. commutatum*, *Myrtus communis* and occasional cork oaks. In the areas of lowest elevation and the highest soil humidity, vegetation is dominated by heathland or ‘monte negro’ species, such as *Erica ciliaris*, *E. scoparia*, *Stauracanthus genistoides*, *Calluna vulgaris*, *M. communis*, *Ulex minor*, *Rubus ulmifolius*, *Ruscus aculeatus* and *Pteridium aquilinum* and occasional cork oaks. At the edge of the marsh is a strip of eutrophic grassland with patches of hygrophytic vegetation (e.g. *Juncus* spp., *Ulex* spp., *R. ulmifolius*, *P. aquilinum*, etc.) known as the ‘vera’, situated in the transition zone between the scrubland and the seasonally flooded grassland of the marsh.

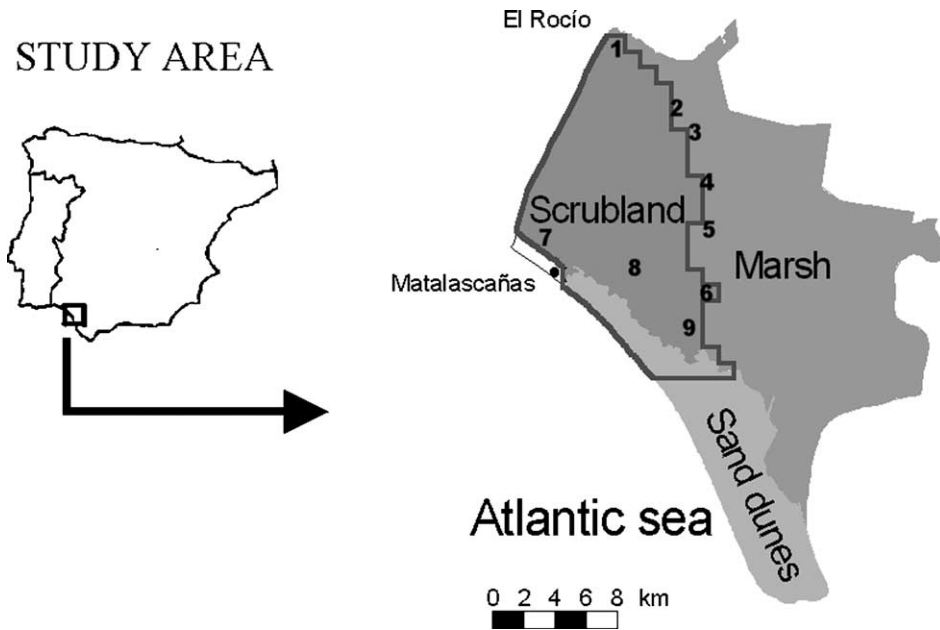


Fig. 1. The location of Doñana NP in Spain and houses in the Park (see Material and Methods). Houses Codes: (1) Rocina, (2) Los Guardas, (3) Hato Barrera, (4) La Algaida, (5) Martinazo, (6) Chalet, (7) Casa Control, (8) Sta. Olalla, (9) El Puntal.

2.3. Sampling method

In order to maximise the number of species detected when making species lists, it has been recommended to employ a variety of sampling techniques (Espadaler and Lopez-Soria, 1991). Pitfall traps are the most commonly used tool for sampling soil surface ants. Although they have some drawbacks (Southwood, 1978), they generally give a good indication of the relative importance of soil surface species, and can trap ants with very different patterns of daily activity (Cerda and Retana, 1988). In order to reduce quantitative sampling biases due to differences in colony size and foraging behaviour between species, we carried out analyses using presence/absence data of species in traps rather than the abundance of workers caught in traps (Suarez et al., 1998). In

each of the principle habitat types described (*monte blanco*, *monte negro*, transitional *monte blanco*, *vera* and pine plantation), we placed five transects of 10 pitfall traps (i.e. a total of 50 traps per habitat) placed at 5 m intervals along each transect for a period of 48 h. In the human environments (i.e. immediate vicinity of wardens houses and visitors centre), we placed a total of 40 pitfall traps along four transects at each site, also for a duration of 48 h. At each site the transects were placed around the principle dwelling, radiating out in four evenly spaced compass directions. When any of the traps was lost, it was immediately replaced in the same place and for the same period.

Pitfall traps were made from 100 ml plastic containers with a 6 cm diameter. The cups were buried to the rim in soil and filled with 25 ml of water mixed with 10% of glycerine. The traps were placed in summer (July 1990), the season associated with maximum activity of most ant species in these latitudes (Tinaut, 1982; Acosta et al., 1983a; Cerda and Retana, 1988; Jimenez and Tinaut, 1992). In addition, as the frequency of ant species in different communities is closely related to the species composition of the vegetation (Carpintero et al., 2000; Fernandez-Haeger and Rodriguez, 1982), we measured the vegetative cover of each species of shrub and tree over each pitfall trap.

Finally, in July of 1992 and 1993, we repeated pitfall trap sampling in the four houses found to be associated with *L. humile* in 1990 (Martinazo, Santa Olalla, Chalet, La Rocina). The house of Martinazo was also sampled in the summer of 1991.

Table 1
Cross-classification of houses by surrounding natural habitat and whether inhabited. All the uninhabited houses are in the “Vera”

Vegetation types	Inhabited	Uninhabited
Monte blanco	El Puntal Casa Control	
Pine plantation	Rocina	
Vera	Martinazo	La Algaida Los Guardas Hato Barrera
Transitional Monte blanco	Chalet	
Monte Negro	Sta. Olalla	

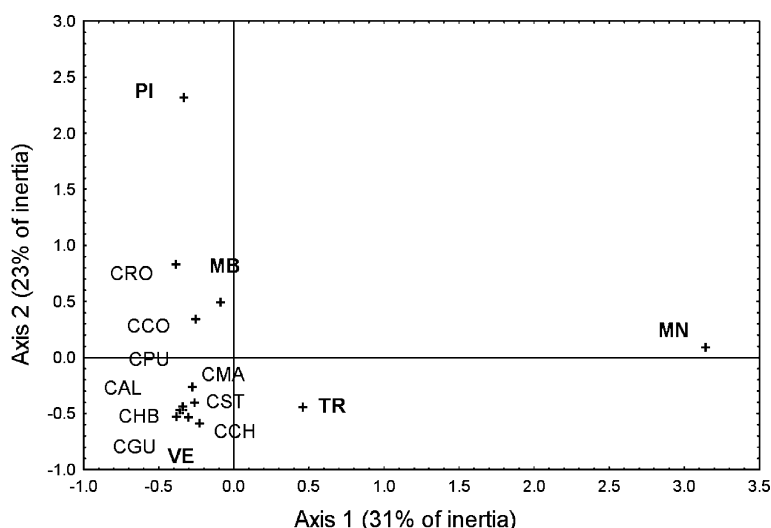


Fig. 2. Study sites plotted against the first two axes obtained from a factorial correspondence analysis of site and vegetative cover over traps. MB—*monte blanco*, PI—pine plantation, MN—*monte negro*, TR—transitional *monte blanco*, VE—*vera*, CAL—house of La Algaida, CHB—house of Hato Barrera, CGU—house of Los Guardas, CPU—house of Puntal de Los Gonzalez, CCO—control house, CCH—Chalet, CMA—house of Martinazo, CST—house of Santa Olalla, CRO—visitors centre at La Rocina.

covered by grasses or herbaceous plants), although they are influenced to a certain degree by the natural habitats where they are located.

3.2. Ant fauna

We identified 31 species of ants which varied in abundance between sites (Table 3). Species richness varied between 5 (in the *vera* habitat and two houses in which *L. humile* was found: La Rocina and Chalet) to 14 (transitional *monte blanco*). The highest values of diversity were found in two natural habitats (*monte blanco* and transitional *monte blanco*), whilst the lowest values were found in two of the houses associated with *L. humile* (La Rocina and Chalet). The results show that considerable variation in species richness and diversity exists within both natural and human habitats.

In order to identify associations between habitat types and ant species composition, we carried out a factorial correspondence analysis using presence/absence of ant species in traps. The first axes accounted for 70.16% of the total inertia, and the first two 50.21% (Total iner-

tia = 2.067, $\chi^2 = 3087$, d.f. = 390, $P < 0.0001$). The biplot of the first two axes (Fig. 3) showed the following patterns:

- (1) The xerophytic habitats (pine plantation and *monte blanco*) appear on the positive side of axis 1, and the hygrophytic habitats (transitional *monte blanco*, *vera* and *monte negro*) on the negative side of axis 1. This shows that the ant fauna is strongly influenced by habitat type and soil humidity in the natural habitats. Although the house of Santa Olalla is situated within *monte negro* habitat, the majority of traps (92.5%) were located in sand or grassland, making its ant fauna more closely related to that found around other houses than *monte negro* habitat.
- (2) The houses of La Rocina and Chalet were comparable in the large abundance of *L. humile*, and for their distance from all other habitats, both natural and human.
- (3) The rest of the houses and natural habitats appear in a large group in the centre of the plot.

Except for the houses of La Rocina and Chalet, the pattern of ant fauna between sites was similar to that of

Table 3

Species richness (S), diversity (H' , Shannon–Weaver index) and equitability (J') by habitat class type (calculated using presence/absence of species in traps)

	Natural habitats					Uninhabited houses			Inhabited houses without <i>L. humile</i>			Inhabited houses with <i>L. humile</i>		
	TR	MN	PI	MB	VE	CHB	CGU	CAL	CPU	CCO	CSA	CMA	CRO	CCH
S	14.0	11.0	12.0	7.0	5.0	11.0	11.0	8.0	12.0	12.0	11.0	9.0	5.0	5.0
H'	3.1	3.1	2.9	2.3	1.8	3.0	2.9	2.5	2.9	2.5	2.9	2.7	1.6	1.4
J'	0.8	0.9	0.8	0.8	0.7	0.8	0.8	0.8	0.8	0.7	0.8	0.9	0.7	0.6

Abbreviations same as in Fig. 2. The lowest values of diversity are in the houses with Argentine ant.

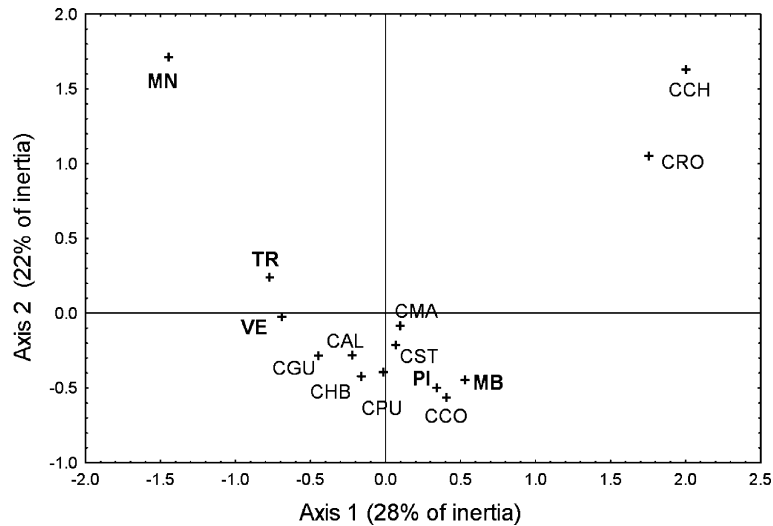


Fig. 3. Study sites plotted against the first two axes obtained from a factorial correspondence analysis of site and composition of ant species in traps. (Abbreviations same as in Fig. 2).

vegetative cover, in that all the houses were grouped together, although they were influenced to some extent by the surrounding natural habitats.

In order to show which species were associated with the proximity of houses, we grouped species by their presence in different areas (Table 4). There were 10 species exclusive to natural habitats, and six only found around houses. The remaining species were divided amongst the three other distribution categories defined in Table 4.

3.3. Inter annual variation in species found in houses associated with the Argentine ant

The annual abundance of species in houses associated with *L. humile* is presented in Table 5. In two of these four houses, there were significant differences in the abundance of some ant species between the first and last year of sampling (Santa Olalla $\chi^2 = 54.31$, d.f. = 10, $P < 0.001$; Martinazo $\chi^2 = 18.76$, d.f. = 8, $P < 0.05$).

However, in the other two houses, there was no temporal change in abundance of *L. humile* or native species (Chalet $\chi^2 = 6.88$, d.f. = 5, $P > 0.05$; Rocina $\chi^2 = 2.93$, d.f. = 5, $P > 0.05$).

In one of the houses (Martinazo) sampling was carried out over four consecutive years, including 1991 when the Argentine ant was found in 11 of the 40 traps set. Thus, in July of each of the 4 years of sampling *L. humile* appeared in 9, 11, 23 and 24 traps. This suggests a rapid initial growth of the Argentine ant population in this site, which then stabilised over the last 2 years of sampling.

In those houses in which the Argentine ant had increased in abundance over time, there tended to be an associated decrease in the abundance of native species. Only *Cataglyphis floricola* seemed to remain unaffected. In the house of Santa Olalla *Crematogaster auberti* did not change in abundance between years, and in the house of Martinazo, *Messor lusitanicus* and *M. maroccanus* actually increased in frequency despite increases

Table 4

Classification of ant species by their occurrence (percentage of traps) in natural and human habitats (i.e. around houses). Some species are exclusively associate to houses

Occur only in natural habitats (100%)	Mostly found in natural habitats (> 66%)	Occur in both habitats (33–66%)	Mostly found around houses (> 66%)	Occur only around houses (100%)
<i>Hypoponera punctatissima</i>	<i>Aphaenogaster gibosa</i>	<i>Aphaenogaster senilis</i>	<i>Messor maroccanus</i>	<i>Messor bouvieri</i>
<i>Myrmica aloba</i>	<i>Leptothorax rabaudi</i>	<i>Tetramorium hispanicum</i>	<i>Messor lusitanicus</i>	<i>Messor hispanicus</i>
<i>Crematogaster scutellaris</i>	<i>Plagiolipsis schmitzii</i>	<i>Crematogaster auberti</i>	<i>Oxyopomyrmex saulcyi</i>	<i>Leptothorax naeviventris</i>
<i>Solenopsis robusta</i>	<i>Lasius niger</i>	<i>Tapinoma erraticum</i>	<i>Tetramorium caespitum</i>	<i>Cataglyphis rosenhaueri</i>
<i>Leptothorax racovitzai</i>	<i>Formica fusca</i>	<i>Cataglyphis floricola</i>	<i>Tapinoma nigerrima</i>	<i>Linepithema humile</i>
<i>Leptothorax tyndalei</i>				<i>Cardiocondyla batesii</i>
<i>Lasius brunneus</i>				
<i>Camponotus pilicornis</i>				
<i>Camponotus lateralis</i>				
<i>Formica subrufa</i>				

in the trap frequency of *L. humile* in both houses. However, these species were mainly found in traps located farthest from the houses, whilst *L. humile* was usually absent from these traps.

It is possible that some ant species are more susceptible than others to competition with *L. humile*. In order to determine if any native species were associated with *L. humile*, we carried out a factorial correspondence analysis using presence/absence data for each species in traps around houses associated with *L. humile*. The first two axes accounted for 90.3% of total inertia (Total inertia = 0.86766, $\chi^2 = 306.28$, d.f. = 36, $P < 0.0001$). In the space defined by the first two axes (Fig. 4), the Argentine ant is shown to be associated principally with

Oxyopomyrmex saulcyi and *Cardiocondyla batesii*, and to a lesser extent, with *Cataglyphis floricola*.

4. Discussion

4.1. Distribution of the Argentine ant

In this study *L. humile* was only found in the immediate vicinity of houses set within the Doñana Park in a variety of natural habitat types, suggesting that the surrounding habitat was not an important factor affecting the presence of *L. humile*. The habitat in the immediate vicinity of all the houses was very similar,

Table 5

Number of traps occupied by each species in 1990, 1991 and 1993 in the four houses where *L. humile* was present (total = 40 traps). In the houses occupied in 1990 by the Argentine ant its occupation stayed

	SANTA OLALLA			MARTINAZO			CHALET			LA ROCINA		
	1990	1992	1993	1990	1992	1993	1990	1992	1993	1990	1992	1993
<i>L. humile</i>	3	20	30	9	24	23	34	33	30	35	34	39
<i>C. floricola</i>	7	9	9	30	29	33	9	11	12	35	34	34
<i>T. hispanicum</i>	2	4	0	30	18	21				0	0	1
<i>T. nigerrima</i>	23	8	9	26	11	15						
<i>A. senilis</i>	1	11	0	27	18	24	4	4	3	0	1	0
<i>L. Níger</i>	6	1	0									
<i>M. maroccanus</i>	14	15	2	5	10	17	2	0	0	2	0	2
<i>T. caespitum</i>	6	2	0	3	4	1	1	3	4			
<i>P. schmitzii</i>	2	0	0							0	2	0
<i>C. auberti</i>	2	3	2									
<i>O. saulcyi</i>	1	1	0	1	3	1				6	3	6
<i>M. lusitanicus</i>				14	14	17	0	1	2			
<i>C. batesii</i>										2	5	6
<i>L. racovitzai</i>										0	1	0

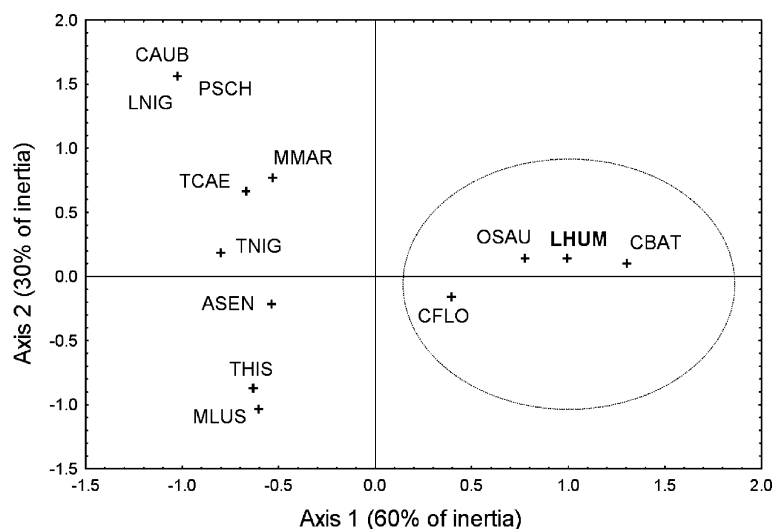


Fig. 4. Ant species found in traps plotted against the first two axes obtained from a factorial correspondence analysis of site (only includes houses occupied by the Argentine ant) and composition of ant species in traps. (CAUB = *C. auberti*, PSCH = *P. schmitzii*, LNIG = *L. niger*, MMAR = *M. maroccanus*, TCAE = *T. caespitum*, TNIG = *T. nigerrima*, ASEN = *A. senilis*, THIS = *T. hispanicum*, MLUS = *M. lusitanicus*, OSAU = *O. saulcyi*, CBAT = *C. batesii*, CFLO = *C. floricola*, LHUM = *L. humile*).

characterised by a sparse cover of vegetation (between 55/60 and 100% of traps located in sand or grassland). The clearing of vegetation around houses may favour the unicolonial Argentine ant in various ways. For example, cleared ground may facilitate range expansion of this species with budding reproduction, by allowing increased mobility of groups of workers and queens (Passera and Aron, 1993).

The next step was to determine whether the ant fauna around houses was more influenced by local habitat structure, or by the surrounding natural habitat, and to what extent native ant community favoured the establishment of *L. humile*. In general, the habitats in the immediate vicinity of houses were no less diverse and/or species rich than natural habitats (Table 3). The surroundings of the houses are very similar in vegetation and fauna and different from the natural vegetation. Ant species richness and diversity around houses did not depend on whether the houses were inhabited, although in those cases with a high abundance of Argentine ant, where there was a decrease in species diversity and richness. However, there was a difference in ant species composition between the immediate vicinity of houses and the surrounding natural habitats. This is shown graphically (Fig. 2), where separate groupings can be identified for the houses with a high abundance of Argentine ants (La Rocina and Chalet), and for the majority of the other houses, including those with a low abundance of Argentine ants, and houses situated in *vera*, *monte blanco* and *monte negro* habitats. These patterns suggest that the cutting of vegetation around houses create local conditions favouring some species and excluding others, leading to species compositions distinct from those in surrounding natural habitats.

When comparing the composition and abundance of species around houses with that of natural habitats (Table 4), we find that:

- (1) The species found in natural habitats and absent or only present in low density around houses, tend to be species associated with relatively humid habitats (*H. punctatissima*, *L. racovitzai*, *L. tyndalei*, *F. subrufa*, *M. aloba*, *A. gibbosa*, *L. niger* and *F. fusca*), forests or scrubland (*C. scutellaris*, *C. pilicornis*, *C. lateralis*, *L. brunneus*, *L. rabaudi* and *P. schmitzii*) (Bernard, 1968; Rodriguez and Fernandez-Haeger, 1983; Tinaut, 1981).
- (2) Species that are common to both houses and natural areas, are amongst the most abundant species in the Park (Carpintero et al., 2001), and include species typical of xerophytic habitats (*C. floricola*), open habitats (*T. hispanicum*) or opportunist species with a broad habitat range (*A. senilis*, *T. erraticum*, *C. auberti*) (Acosta et al., 1983a; Cerda and Retana, 1988; Retrepo et al., 1985).

- (3) Those species found uniquely or in relatively high abundance around houses include species typical of open habitats (*M. bouvieri*, *M. hispanicus*, *L. naeviventris*, *C. rosenhaueri*, *M. maroccanus*, *M. lusitanicus*, *O. saulcyi*) and opportunist species often associated with man (*T. caespitum*, *T. nigerrima*, *L. humile*) (Pisarski and Czechowski, 1978). *C. batesii* is also found in this group, and is a specialist of relatively unstable substrates (Acosta et al., 1983b).

Therefore, opportunists, generalists or open habitat ant species are found in the immediate vicinity of houses, whilst forest species associated with scrubland and hygrophytic habitats are usually absent. This finding is comparable with studies carried out in urban environments, which show that arboreal species, and species associated with shady or humid conditions are generally absent, whilst ants and other insect species associated with open, dry or semi-dry habitats (Chudzicka et al., 1990), and generalist species (Pisarski and Kulesza, 1982) are relatively common.

Although the houses in the Natural Park cannot be considered as true urban habitats, because they do not have certain diagnostic characteristics such as high human density, reduced quantity of surface and underground water, loss of soil, pollution, removal of indigenous vegetation and introduction of foreign species, increased ground temperatures, etc. they are habitats influenced by human activity, and may be considered as semi-natural areas (McDonnell and Pickett, 1990).

The immediate surroundings of houses are associated with a distinct habitat type and fauna, but the diversity of the ant fauna around houses is not less than that of natural areas in the Park, suggesting that low ant diversity is not a critical factor in determining the establishment of the Argentine ant. In addition, we can reject the hypothesis that low competitive ability of local ant species is key in the establishment of the Argentine ant in this area, since many native species found around houses such as *T. hispanicum*, *M. maroccanus* and *T. nigerrima* form large colonies, show aggressive behaviour, respond to attacks in large numbers, and so are considered as dominant species (Cerda et al., 1998a,b; Hölldobler and Wilson, 1990; Pisarski and Vepsäläinen, 1989). In another study on the coast of France, the Argentine ant has been shown to be able to displace dominant ant species such as *Tetramorium* spp. and *Tapinoma erraticum* (Passera, 1994).

The fact that the Argentine ant is only found in the immediate vicinity of inhabited houses is not because these houses have special environmental conditions or vegetation structure, nor is it due to low ant species diversity. We suggest that the Argentine ant is found in these house because (a) the propagule pressure (rate of arrival of invading individuals) is likely to be higher around inhabited houses due to the constant human

movement of materials from areas outside the Park (Crowell, 1968; Forte, 1956; Passera and Aron, 1993; Woodworth, 1910), (b) houses provide good conditions for initial establishment, including both abiotic factors (humidity, food, etc.) and biotic factors (i.e. absence of other formicids in houses). Argentine ant invasions may begin in houses, where the colony is built up to a sufficient size before expanding its range into new ground (Fellers and Fellers, 1982). In Hawaii, Fluker and Beardsley (1970) showed that *L. humile* does not invade new ground for around 4–6 months after establishment, whilst the colony grows sufficiently to reach an invasive state, when they become very aggressive and start to gain new territory.

Is it possible to determine whether an Argentine ant population is expanding or whether it will invade surrounding natural habitats? Pisarski and Kulesza (1982) have described *L. humile* as a true anthropophilic species. However, in California *L. humile* has appeared not only in altered habitats but also natural woodlands (riverine forest), where they have reduced local species diversity (Holway, 1998a,b; Ward, 1987). Also in California, Suarez et al. (1998) found that the Argentine ant occupied human altered habitats associated with exotic vegetation, paths, etc. but was capable of invading nature reserves with unaltered vegetation, and displacing native ant species. In South Africa, De Kock and Giliomee (1989) found *L. humile* in human altered habitats close to residential areas, but also found that *L. humile* penetrated into natural habitats via roads and paths, regardless of the presence or absence of exotic vegetation.

In Haleakala National Park in Hawaii, Fellers and Fellers (1982) also found *L. humile* associated with human altered habitats around the Park offices and laboratories, never being found more than 1 km from these buildings. However, they did not rule out the possibility that they could spread further. Cole et al. (1992) suggested that the Argentine ant has the potential to occupy a much larger area of Haleakala National Park than that observed in the previous study mentioned. These studies show that the Argentine ant is capable of invading natural habitats from nearby human altered habitats.

The abundance of paths and roads may be an important factor facilitating the rapid spread of the Argentine ant even in very large nature reserves, not only by creating favourable habitats along roadsides, but also by speeding up dispersal via passive transport in automobiles. The factors that appear to be most important in limiting range expansion of the Argentine ant are abiotic, including low temperatures and prolonged droughts (De Kock et al., 1992; Fellers and Fellers, 1982; Forte, 1956; Hertzner, 1930; Holway, 1998a; 1999; Majer, 1994; Suarez et al., 1998; Tremper, 1976; Van Schagen et al., 1994; Ward, 1987; Woodworth, 1910).

All these studies lead us to believe that the Argentine ant has the potential to occupy favourable natural habitats in Doñana, particularly the relatively moist habitats such as the areas surrounding pools or patches of *monte negro* near the edge of the marsh.

4.2. The impact of the Argentine ant on native species

In the four sites invaded by the Argentine ant, two distinct patterns were observed. In two of the houses there was an increase in the abundance of *L. humile* accompanied by the disappearance or decrease in abundance of native species, whilst in the other two houses, there was no temporal trend in the abundance of the different species present (Table 5). These different patterns may reflect different stages of establishment of the Argentine ant in these sites: recently invaded sites (Santa Olalla and Martinazo) may be associated with a rapid expansion of the Argentine ant population and a corresponding decrease in the abundance of native species, whilst long established populations (Chalet and Rocina) may be associated with more stable population dynamics, as observations of the Argentine ant population in the house of Martinazo suggest. In Bermuda, Brandao and Paiva (1994) and Haskins and Haskins (1988) found that the range expansion of *L. humile* decreased at high population densities. A similar pattern of population growth is observed in other ant species, supporting the hypothesis that population growth of colonies of social insects is regulated by density-dependent processes (Henderson et al., 1989).

The Argentine ant is likely to vary in its impact on native species, displacing some species sooner than others. *Cardiocondyla batesii* and *Oxyopomyrmex saulcyi*, which are trapped in low frequencies and characterised by small body and colony size (Bernard, 1968; Tinaut, 1981), seem to belong to the latter category, often being found in the presence of *L. humile*. Although *Cataglyphis floricola* is caught in relative high numbers in the same traps as *L. humile*, it is probable that these two species have little direct interaction, since *C. floricola* is active in the hottest part of the day when all other species are inactive. In addition, *C. floricola* can move long distances from its nest in search of food, such that co-occurrence of workers of the two species in traps does not necessarily denote proximity of colonies (unpublished data). In general, species that are able to co-exist with dominant species (abundant, aggressive, territorial, etc.) (Greenslade, 1976), are those that occupy a low position in the competitive hierarchy, usually defending only their nests and often occupying sub-optimal habitats (Pisarski and Vepsäläinen, 1989).

Other authors have found similar relationships, such as Holway (1998a), Suarez et al. (1998) and Sanders et al. (2001), who have described different ant species

as being more or less vulnerable to the presence of *L. humile*. For example, *Prenolepis imparis* is little affected by the presence of the Argentine ant due to the seasonal difference of its peak activity period. Another ant species, the small (approximately 2 mm in length) subterranean *Leptothorax andrei*, has also been shown to be relatively resistant to Argentine ant invasions, probably due to lack of niche overlap. Similarly, *Plagiolepis pygmaea* and *Solenopsis fugax* were found to persist in areas colonised by *L. humile* in Portugal and the south of France (Chopard, 1921; Passera, 1994).

This type of pattern has been described for other invasive ant species such as *Solenopsis invicta*, *Pheidole megacephala*, *Paratrechina longicornis* or *Wasmannia auropunctata*, which generally displace ant species with similar ecological requirements, whilst other species, which may have different requirements, or occupy a lower hierarchical position or occupy sub-optimal niches, are more resistant to the presence of these invaders (Haskins and Haskins, 1988; Morris and Steigman, 1993; Phillips et al., 1987; Porter and Savignano, 1990; Stein and Thorvilson, 1989; Tennant, 1994; Wetterer et al., 1999).

Finally, it seems certain that man is the principle dispersal agent for the Argentine ant (Passera, 1994). Many methods of control are being tested against this species and other pest ants (Vander Meer et al., 1990; Williams, 1994) but actually the best strategies for limiting the spread of this and other invasive species to ecologically sensitive areas should include measures to avoid the arrival of invasive propagules carried by man, for example, by checking materials brought into protected areas, and limiting vehicle and/or personal access. In addition, it is important to establish monitoring programs so that infestations can be rapidly detected, to have contingency eradication or control programs and to reduce the area of habitats conducive to colonisation by invasive species (e.g., reducing disturbed areas) (De Kock and Giliomee, 1989; Macdonald, 1990; Newell and Barber, 1913; Reimer, 1994; Woodworth, 1910).

Acknowledgements

We would like to thank Mariano J. Rodriguez, Mariano Bosch, Diego Jordano, Jaime Aperribay, Claudia Keller and Antonio Priego for their help with field work, and Catalina Ramirez for sorting samples. David Williams gave much of the bibliographic material, and Alberto Tinaut clarified uncertainties in the ant taxonomy. We also thank all our colleagues and the staff of Doñana for their kindness and help. This study was supported by an F.P.I. grant from Comunidad Autónoma de Andalucía to S. Carpintero.

References

- Acosta, F.J., Martínez, M.D., Serrano, J.M., 1983a. Contribución al conocimiento de la mirmecofauna del encinar peninsular. II: principales pautas autoecológicas. Boletín de la Asociación española de Entomología 7, 297–306.
- Acosta, F.J., Morales, M., Serrano, J.M., 1983b. Capacidad de transcripción de una mirmecocenosis en un medio adverso. Boletín de la Asociación española de Entomología 7, 151–158.
- Bernard, F., 1968. Les fourmis (Hymenoptera Formicidae) d'Europe occidentale et septentrionale. Faune de l'Europe et du Bassin Méditerranéen. Ed. Masson.
- Brandao, C.R., Paiva, V.S., 1994. The Galapagos ant fauna and the attributes of colonizing ant species. In: Williams, D.F. (Ed.), Exotic Ants. Biology, Impact, and Control of Introduced Species. Westview Press, Oxford, pp. 1–10.
- Carpintero, S., Tinaut, A., Herrera-Grao, A., Ferreras-Romero, M., 2000. Estudio faunístico y ecológico de las hormigas (Hymenoptera: Formicidae) de la cuenca superior del río Hozgarganta (Parque Natural Los Alcornocales, Cádiz). Boletín de la Asociación española de Entomología 24 (3–4), 125–138.
- Carpintero, S., Tinaut, A., Reyes-López, J., Arias de Reyna, L., 2001. Estudio faunístico de los formicidos (Hymenoptera, Formicidae) del Parque Nacional de Doñana. Boletín de la Sociedad Española de Entomología 25 (1/2), 133–152.
- Cerda, X., Retana, J., 1988. Descripción de la comunidad de hormigas de un prado sabanoide en Canet del Mar (Barcelona). Ecología 2, 333–341.
- Cerda, X., Retana, J., Cros, S., 1998a. Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance. Functional Ecology 12, 45–55.
- Cerda, X., Retana, J., Manzaneda, A., 1998b. The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. Oecologia 117 (3), 404–412.
- Chopard, L., 1921. La fourmi d'Argentine *Iridomyrmex humilis* var. *Arrogans* Santschi dans le midi de la France. Annales des Epiphyties 7, 237–266.
- Chudzicka, E., Pisarski, B., Skibinska, E., 1990. Origin and variability of the fauna of urbanized areas. Fragmenta Faunistica 34 (1), 1–16.
- Cole, F.R., Medeiros, A.C., Loope, L.L., Zuehlke, W.W., 1992. Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrublands. Ecology 73, 1313–1322.
- Crowell, K.L., 1968. Rates of competitive exclusion by the Argentine ant in Bermuda. Ecology 49, 551–555.
- De Kock, A.E., Giliomee, J.H., 1989. A survey of the Argentine ant, *Iridomyrmex humilis* (Mayr), (Hymenoptera: Formicidae) in South African fynbos. Journal of the Entomological Society of Southern Africa 52 (1), 157–164.
- De Kock, A.E., Giliomee, J.H., Pringle, J.L., Majer, J.D., 1992. The influence of fire, vegetation age and Argentine ant (*Iridomyrmex humilis*) on ant communities in Swartboskloof. In: Van Wilgen, B.W., Richardson, D.M., Kruger, F.J., Van Hensbergen, H.J. (Eds.), Fire in South African Fynbos: Ecosystem, Community, and Species Response at Swartboskloof. Springer-Verlag, Berlin, pp. 203–215.
- Espadaler, X., Lopez-Soria, L., 1991. Rareness of certain Mediterranean species: fact or artifact? Insectes Sociaux 38, 365–377.
- Fellers, J.H., Fellers, G.M., 1982. Status and distribution of ants in the Crater District of Haleakala National Park. Pacific Science 36 (4), 427–437.
- Fernández-Haeger, J., Rodríguez, A., 1982. Les peuplements de fourmis dans la Sierra Morena Centrale (Espagne) rapports avec l'exposition et la végétation. Insectes Sociaux 29 (2), 358–368.
- Fluker, S.S., Beardsley, J.W., 1970. Sympatric associations of three ants: *Iridomyrmex humilis*, *Pheidole megacephala* and *Anoplolepis longipes* in Hawaii. Annals Entomological Society of America 63, 1290–1296.

- Forte, P.N., 1956. Some observations on the Argentine Ant campaign in Western Australia. *Journal of Agriculture of Western Australia* 5 (3), 1–8.
- Gaussen, H., 1968. Les indices serothermique et hygrothermique en Peninsule Hispanique et en Africa du Nord partie N.W. *Collectanea Botánica* 7, 499–504.
- Greenslade, P.J.M., 1976. The meat ant *Iridomyrmex purpureus* as a dominant member of ant communities. *Journal of Australian Entomological Society* 15, 237–240.
- Haskins, C.P., Haskins, E.F., 1988. Final observations on *Pheidole megacephala* and *Iridomyrmex humilis* in Bermuda. *Psyche* 95, 177–184.
- Henderson, G., Wagner, R.O., Jeanne, R.L., 1989. Prairie ant colony longevity and mound growth. *Psyche* 96 (3–4), 257–268.
- Hertzer, L., 1930. Response of the Argentine ant (*Iridomyrmex humilis* Mayr) to external conditions. *Annals Entomological Society of America* 23, 597–600.
- Hölldobler, B., Wilson, E.O., 1990. *The Ants*. Springer-Verlag, Berlin.
- Holway, D.A., 1998. Factors governing rate of invasion: a natural experiment using Argentine ants. *Oecologia* 115, 206–212.
- Holway, D.A., 1998. Effects of Argentine ant invasion on ground-dwelling arthropods in Northern California riparian woodlands. *Oecologia* 116 (1/2), 252–258.
- Holway, D.A., 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology* 80 (1), 238–251.
- Jimenez, J., Tinaut, J.A., 1992. Mirmecofauna de la Sierra de Loja (Granada). *Orsis* 7, 97–111.
- Macdonald, I.A.W., 1990. Strategies for limiting the invasion of protected areas by introduced organisms. *Monographs in Systematic Botany from the Missouri Botanical Garden* 32, 189–199.
- Macdonald, I.A.W., Graber, D.M., DeBenedetti, S., Groves, R.H., Fuentes, E.R., 1988. Introduced species in nature reserves in Mediterranean-type climatic regions of the world. *Biological Conservation* 44, 37–66.
- Majer, J.D., 1994. Spread of Argentine ants (*Linepithema humile*), with special reference to western Australia. In: Williams, D.F. (Ed.), *Exotic Ants. Biology, Impact, and Control of Introduced Species*. Westview Press, Oxford, pp. 161–173.
- McDonnell, M.J., Pickett, S.T.A., 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology* 71 (4), 1232–1237.
- Morris, J.R., Steigman, K.L., 1993. Effects of polygyne fire ant invasion on native ants of a Blackland prairie in Texas. *The Southwestern Naturalist* 38 (2), 136–140.
- Newell, W., Barber, T.C., 1913. The Argentine Ant. *Bulletin Bureau of Entomology*. US Department of Agriculture 122, 1–98.
- Newman, E.I., 1993. *Applied Ecology*. Blackwell Scientific Publications, Oxford.
- Passera, L., 1994. Characteristics of tramp species. In: Williams, D.F. (Ed.), *Exotic Ants. Biology, Impact, and Control of Introduced Species*. Westview Press, Oxford, pp. 23–43.
- Passera, L., Aron, S., 1993. Social control over the survival and selection of winged virgin queens in an ant without nuptial flight: *Iridomyrmex humilis*. *Ethology* 93, 225–235.
- Phillips, S.A., Rogers, W.M., Wester, D.B., Chandler, L., 1987. Ordination analysis of ant faunas along the range expansion of the red imported fire ant in South-Central Texas. *Texas Journal of Agriculture and Natural Resources* 1, 11–15.
- Pisarski, B., Czechowski, W., 1978. Influence de la pression urbaine sur la myrmecofaune. *Memorabilia Zoologica* 29, 109–128.
- Pisarski, B., Kulesza, M., 1982. Characteristics of animal species colonizing urban habitats. *Memorabilia Zoologica* 37, 71–77.
- Pisarski, B., Vepsäläinen, K., 1989. Competition hierarchies in ant communities (Hymenoptera, Formicidae). *Annales Zoologici* 42 (13), 321–328.
- Porter, S.D., Savignano, D.A., 1990. Invasion of polygyne ants decimates native ants and disrupts arthropod community. *Ecology* 71 (6), 2095–2106.
- Reimer, N.J., 1994. Distribution and impact of alien ants in vulnerable Hawaiian ecosystems. In: Williams, D.F. (Ed.), *Exotic Ants. Biology, Impact, and Control of Introduced Species*. Westview Press, Oxford, pp. 11–22.
- Retrepo, C., Espadaler, X., De Haro, A., 1985. Contribución al conocimiento faunístico de los formicidos del Macizo de Garraf (Barcelona). *Orsis* 1, 113–129.
- Rodríguez, J., 1991. Las mariposas del Parque Nacional de Doñana. *Biología y Ecología de Cyaniris semiargus y Plebejus argus*. PhD thesis, Department of Ecology, University of Cordoba (Spain).
- Rodríguez, A., Fernández-Haeger, J., 1983. Empleo del análisis de clasificación para la detección de grupos de especies afines en una comunidad de hormigas. *Studia Oecologica* 4, 115–124.
- Sanders, N.J., Barton, K.E., Gordon, D.M., 2001. Long-term dynamics of the distribution of the invasive Argentine ant, *Linepithema humile*, and native ant taxa in northern California. *Oecologia* 127, 123–130.
- Southwood, T.R.E., 1978. *Ecological Methods*. Chapman and Hall, London.
- Stein, M.B., Thorvilson, H.G., 1989. Ant species sympatric with the red imported fire ant in Southeastern Texas. *Southwestern Entomologist* 14 (3), 225–231.
- Suarez, A.V., Bolger, D.T., Case, T.J., 1998. Effects of fragmentation and invasion on native ant communities in coastal Southern California. *Ecology* 79 (6), 2041–2056.
- Tennant, L.E., 1994. The ecology of *Wasmannia auropunctata* in primary tropical rainforest in Costa Rica and Panama. In: Williams, D.F. (Ed.), *Exotic Ants. Biology, Impact, and Control of Introduced Species*. Westview Press, Oxford, pp. 80–90.
- Tinaut, A., 1981. Estudio de los Formicidos de Sierra Nevada. PhD thesis, Department of Biology, University of Granada (Spain).
- Tinaut, A., 1982. Evolución anual de la mirmecocenosis de un encinar. *Boletín de la Estación Central de Ecología* 11 (22), 9–56.
- Tremper, B.S., 1976. Distribution of the Argentine Ant, *Iridomyrmex humilis* Mayr, in Relation to Certain Native Ants of California, Physiological, and Behavioral Aspects. PhD thesis, University of California, Berkeley.
- Vander Meer, R.K., Jaffe, K., Cedeno, A. (Eds.), 1990. *Applied Myrmecology. A World Perspective*. Westview Press, Oxford.
- Van Schagen, J.J., Davis, P.R., Widmer, M.A., 1994. Ant pests of western Australia, with particular reference to the Argentine ant (*Linepithema humile*). In: Williams, D.F. (Ed.), *Exotic Ants. Biology, Impact, and Control of Introduced Species*. Westview Press, Oxford, pp. 174–180.
- Ward, P.S., 1987. Distribution of the introduced Argentine Ant (*Iridomyrmex humilis*) in natural habitats of the lower Sacramento Valley and its effects on the indigenous ant fauna. *Hilgardia* 55 (2), 1–17.
- Wetterer, J.K., Miller, S.E., Wheeler, D.E., Olson, C.A., Polhemus, D.A., Pitts, M., Ashton, I.W., Himler, A.G., Yospin, M.M., Helms, K.R., Harker, E.L., Gallaher, J., Dunning, C.E., Nelson, M., Litsinger, J., Southern, A., Burgess, T.L., 1999. Ecological dominance by *Paratrechina longicornis* (Hym.: Form.) an invasive tramp ant, in Biosphere 2. *Florida Entomologist* 82 (3), 381–388.
- Williams, D.F. (Ed.), 1994. *Exotic Ants. Biology, Impact, and Control of Introduced Species*. Westview Press, Oxford.
- Woodworth, C.W., 1910. The Control of the Argentine Ant. *Bulletin Agricultural Experiment Station, College of Agriculture, Berkeley, University of California*, 207, 51–82.