

**Numerical Dominance of the Argentine Ant vs Native Ants  
and Consequences on Soil Resource Searching in  
Mediterranean Cork-Oak Forests  
(Hymenoptera: Formicidae)**

by

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ABSTRACT

This study is focused on the dominance exerted by the invasive Argentine ant over native ants in a coastal Mediterranean area. The impact of this invasive ant on native ant assemblages and its consequences on total ant biomass and on the intensity of habitat exploration were evaluated. Foraging ants were observed and their trajectories recorded during 5-minute periods in two study zones, one invaded and the other non-invaded. Ant species detected, ant worker abundance, ant biomass and the intensity of soil surface searching done by ants were compared between the two zones. The Argentine ant invasion provoked a drastic reduction of the ant species richness. Apparently only one native ant species is able to coexist with the Argentine ant, the cryptic *Plagiolepis pygmaea*. Ant worker abundance was also modified after the invasion: the number of Argentine ant workers detected, which represented 92% of the invaded zone, was two times higher than the number of native ant workers detected in the non-invaded zone. The total ant biomass was inversely affected, becoming four times lower in the invaded zone highly dominated by *Linepithema humile*. The higher number of Argentine ant workers and their fast tempo of activity implied an alteration of the intensity of soil surface searching: scanning by the Argentine ants in the invaded zone was higher than that done by the native ants in the non-invaded zone, and the estimated time for a complete soil surface scan was 64 minutes in the invaded zone and 108 minutes in the non-invaded zone. Consequently, resources will be discovered faster by ants in the invaded zone than in the non-invaded zone. The increase of the mean temperature and the decrease of the relative humidity from May to August reduced the ant activity in the two study zones but this reduction was greater in the invaded zone.

Keywords: Ant biomass, biological invasion, habitat exploration, *Linepithema humile*, Mediterranean region, numerical dominance.

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## INTRODUCTION

Ants are known to compete in transitive hierarchies, where the better behavioral competitors exclude subordinate species (Human & Gordon 1996, 1997, Hoffmann *et al.* 1999, Holway & Suarez 1999, Morrison 2000). This interspecific competition has been shown to be a key factor affecting structure and dominance in ant communities (Levings 1982, Fellers 1987, Savoilanen & Vepsäläinen 1988, Hölldobler & Wilson 1990, Andersen 1992, 2000). The strategies used by ant species to coexist in a community with other species contesting for many of the same resources can be classified into two categories: exploitative ability (the localization and utilization of resources before competitors) and behavioral dominance (by attacking and/or avoiding competitors at resources) (Davidson 1998). The evolutionary trade-off between these two competitive abilities allows competitor species to persist in ant communities. However, when a species is not bundled by this trade-off, it becomes competitively dominant over the rest, and can cause the displacement of competitors. Some invasive ant species base their success in colonized areas on the breakdown of this trade-off (Davidson 1998, Holway 1999, Holway *et al.* 2002a). The combination of dominance of resources and behavioral dominance in interactions with other species implies an ecological dominance of these invaders over native species, and usually causes the displacement of some native ant species (Porter & Savignano 1990, Cammell *et al.* 1996, Human & Gordon 1997, Holway 1998a, Hoffmann *et al.* 1999, Gómez & Oliveras 2003), leaving these invasive species to dominate the community biomass. The dominance of the community biomass has been proposed by Begon *et al.* (1996) as a descriptive trait for ecologically dominant species.

As well as the interspecific competition, environmental factors (mainly temperature) have been proven to be of great importance in the organization of ant community assemblages (Cerdá *et al.* 1997, 1998, Cros *et al.* 1997, Bestelmeyer 2000). Thus, in Mediterranean communities, where environmental factors show important daily and seasonal variations, the limited thermal tolerance of behaviorally dominant species with respect to subordinate species disrupts the expected transitive hierarchies (Cerdá *et al.* 1997).

The Argentine ant (*Linepithema humile* Mayr) represents an example of success due to the breakdown of the trade-off between exploitative and encounter competition (Davidson 1998). This well-known invasive ant species (McGlynn 1999a) originates from south of the Parana River in Argentina (Tsutsui *et al.* 2001) and has been introduced in various

zones of the world due to human commercial activities (Hölldobler & Wilson 1990, Suarez *et al.* 2001). Its distribution range now includes areas with Mediterranean-type climates throughout the world (Passera 1994, Suarez *et al.* 1998). Although its rapid expansion in invaded zones has been facilitated by human habitat alteration (Suarez *et al.* 1998), there is increasing evidence of its ability to occupy non-altered habitats (Cole *et al.* 1992, Human & Gordon 1996, Holway 1998b). Worldwide, *L. humile* has decimated native ant populations where it has been introduced (Cammell *et al.* 1996, Human & Gordon 1997, 1999, Suarez *et al.* 1998, Holway 1999, Gómez & Oliveras 2003) through intense interference and exploitative competition (Human & Gordon 1996, Davidson 1998, Holway 1999). In fact, the native ant community is probably the first animal group to suffer the impact of the Argentine ant's invasion.

The potential consequences of the impoverishment and homogenization of the ant community caused by the Argentine ant invasion are diverse and comprise different ecological processes in which ants are implicated (Holway *et al.* 2002a). The rates of resource utilization almost surely vary, due in part to different requirements of the invader species and in part to their different abilities with respect to native species. The level of impact of these changes will depend on the degree to which the Argentine replaces and assumes the tasks of the displaced native ants. Thus, although the invader species may assume some roles at the same level as the native species, in most processes the invaders are probably bad replacements for the natives, by defect or by excess in assuming their tasks.

The reduction of ant species richness in the invaded areas is one of the most easily perceptible changes following the invasion. But other less noticeable changes concerning the global ant community, such as the total ant biomass and the intensity of ant activities, in both spatial and temporal terms, could also occur after the invasion. An analysis of these community characteristics in both invaded and non-invaded areas would help to better understand some of the consequences of the invasion in different ecological processes.

In the present study we analyze the level of alteration of the ant community after the Argentine ant invasion by comparing two close Mediterranean cork-oak forest zones, one invaded and the other non-invaded by the Argentine ant. Our first aim is to quantify the expected reduction of the ant species richness caused by the invasion. Subsequently, the questions addressed are: 1) Is the total ant community biomass different in invaded and in non-invaded zones?; 2) Is the intensity of soil surface resource searching in invaded zones different

than in non-invaded zones?; 3) Does the intensity of soil surface resource searching vary seasonally and/or according to environmental conditions in invaded and non-invaded zones?

## MATERIALS AND METHODS

### **Study area**

This study was carried out during May, June, July, and August 2003 in the Serra Llonga, in the southern edge of the Gavarres Massif, near the village of Castell d'Aro (NE Spain) (41° 49' N, 3° 00' E). The study area is 4 km from the Mediterranean coast. The climate of this region is Mediterranean sub-humid, with 627 mm of annual rainfall, a minimum monthly average temperature in January (7.2 °C) and a maximum in July (22.6 °C). In this area the invaded and the non-invaded zones are in close proximity. The Argentine ant distribution in the study area is concentrated principally in those zones next to urbanized areas from where its access and subsequent expansion in less-altered areas started. Both study zones are situated at elevations of 250 m and vegetation is open cork oak secondary forests dominated by *Quercus suber* (L.), *Quercus ilex* (L.), *Erica arborea* (L.), *Cistus monspeliensis* (L.), *Cistus salvifolius* (L.), and *Arbutus unedo* (L.). The relative proximity, as well as to the similar characteristics of vegetation, face, slope, and altitude of the two study zones allow us to assume that the composition of the native ant community previous to the invasion in the now invaded zones would have to be very similar to that found in the non-invaded zone.

### **Soil surface searching by ants**

The intensity of soil surface searching by ants was evaluated as in Espadaler and Gómez (1997). The trajectory made by individual ants during a sampling period of 5 minutes was drawn on a 10 x 10 cm square of acetate sheet placed on a wire frame 5 cm from the soil. A single ant was followed and its trajectory traced all the time it foraged under the sampling surface even if more than one ant was present. If the ant we were tracing left the sampling area before the 5 minutes were over, the first new incoming ant was followed and so on. This constituted a sample. Each sampling point was randomly selected, and samples were taken throughout an extensive area in the two study zones. Trajectories for each ant species were color coded. Two consecutive daily samplings (one in the invaded zone and one in the non-invaded zone) were done monthly during the ants' highest activity period (May, June, July and August 2003). Sampling began at 8:00 in the morning and ended at 19:00 in the evening. A total of 482 5-minute samples (half of them in each zone) were taken. The number of samples

taken each hour was the same in the two study zones. To discard environmental effects, temperature and relative humidity corresponding to the samples taken were compared between the two study zones and the four sampling months. Data were obtained from the meteorological station of Castell d'Aro, situated near to the study zone. The station provides environmental data in means for each 30-minute period. Each 5-minute sample was assigned with its corresponding 30-minute mean temperature and humidity, thus having the same number of data for each environmental variable as of samples ( $n = 482$ ). Both variables were log10-transformed prior to analysis to improve homocedasticity. Neither mean temperature nor humidity during the 5-minute samples taken were different between the two study zones (two-way ANOVA: Temperature,  $F_{1,455} = 1.92$ ,  $P = 0.167$ ; Humidity,  $F_{1,455} = 0.04$ ,  $P = 0.841$ ), but differences were detected between sampling months due to normal fluctuations throughout the year (two-way ANOVA: Temperature,  $F_{3,455} = 809.72$ ,  $P < 0.001$ ; Humidity,  $F_{3,455} = 734.22$ ,  $P < 0.001$ ) (Fig. 1). A measure of the soil surface searched by the ants was estimated from the distance of the trajectories and the antennal gap (maximum distance between tips of antennae) of each ant species. The distance was measured running the ant trajectories on the acetate sheets using a curvimeter with a precision of 0.5 cm. The antennal gap was obtained from the video registration of live individuals of the different ant species foraging over a graph paper sheet into artificial nests and was measured on still images from the film when the two antennae were completely open. The number of ant individuals filmed varied between species because some of them were difficult to find (see Table 1). In some ant species only one individual was measured so the distance is not absolutely representative, but this does not apply to the most represented species so final results were not greatly affected. Intraspecific overlaps of trajectories were calculated as a quadrature of side "antennal gap" and were discounted from the estimated surface searched. From this calculation for all samples, we estimated the mean surface searched by each species for each 5-minute sample. From the velocity of soil surface searching we estimated the time needed by ants for a complete search of the soil surface (Tr) as:  $Tr = S \cdot SS^{-1}$ , where S is the 10 x 10 cm surface sample to be scanned and SS the mean searched surface. Finally, the number of ant trajectories was taken as a measure of the ant worker abundance.

#### **Ant assemblages' biomass**

The ant assemblages' biomass was also considered. We used as a biomass measure the data provided in the biomass data base for Iberian

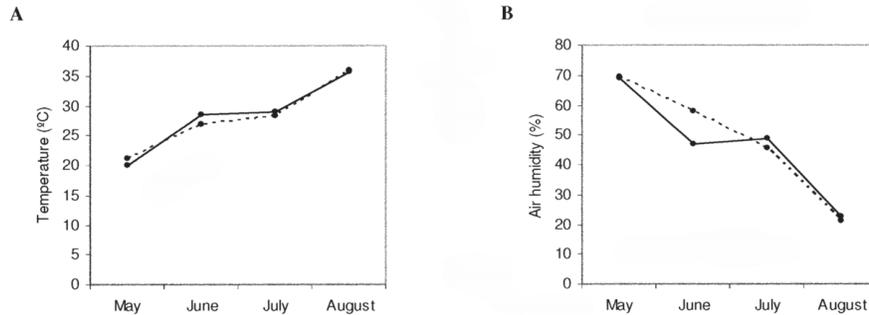


Fig. 1. Mean temperature (A) and mean air humidity (B) during the sampling periods at the two study zones by the four sampling months. Invaded zone in broken lines and non-invaded zone in solid lines.

ants generated by Gómez and Espadaler (2000). They followed a two-step process to estimate the ant species biomass: (1) head length (HL) of workers was directly measured under a stereoscopic microscope to the next 0.006 mm for the smallest ants (up to 1.3 mm HL;  $n = 110$  species) or the next to 0.013 mm for bigger ants ( $n = 32$  species); in 95 species HL was taken directly from published information; (2) dry body mass was then obtained by applying the transformation from Kaspari and Weiser (1999): dry body mass in g ( $M$ ) =  $(4.7297 \cdot 10^{-4}) \cdot HL^{3.179}$ . In polymorphic species, the minimum and maximum were taken and the mean used. A measure of the biomass of each species observed in the study area was then obtained multiplying the species mass by its abundance (number of observed trajectories). This is not a measure of the total ant biomass but is limited to diurnal above-ground foraging workers.

#### Abiotic conditions influence

As ant activity is highly dependent on environmental factors, correlations between the daily means of the activity variables measured (number of ant trajectories, soil surface searching, and ant biomass) and the daily means of temperature and humidity were analyzed using the Pearson's correlation coefficient.

#### Statistical analysis

The mean soil surface searched, the mean ant worker abundance and the mean ant biomass were compared between zones and between sampling months using GLM Univariate Model I Analysis of Variance (ANOVA) and taking each 5-minute sample as a replicate. Data were log<sub>10</sub>-transformed prior to analysis to improve homocedasticity. All statistical analyses were performed using the SPSS package for Windows version 11.5 (SPSS Inc).

## RESULTS

### Ant species assemblages

The total number of ant species detected was far lower in the invaded zone compared vs the non-invaded zone (Table 1). The number of ant species presented a decreasing tendency from May to August in the two zones with the exception of a peak in June in the non-invaded zone (Fig. 2A). In the invaded zone only one species, the invasive *L. humile*, was detected in August.

### Worker abundance and ant biomass

The mean number of ant workers per 5-minute sample detected in the invaded zone (3.99 0.32; mean SE) was more than two times higher than in the non-invaded zone (1.85 0.14) (ANOVA zone effect:  $F_{1,474} = 17.20$ ,  $P < 0.001$ ) (Fig. 2B). In the invaded zone the worker abundance was highly dominated by *L. humile* (92.2% of total ant trajectories). Moreover, its own abundance doubled the number of all native ant workers in the non-invaded zone. In the non-invaded zone the most abundant species was *Pheidole pallidula* (Nylander) with 46.6% of the total ant trajectories. The worker abundance varied between months (ANOVA month effect:  $F_{3,474} = 33.48$ ,  $P < 0.001$ ) decreasing from May to August in the two zones (with the exception of a slight peak in June in the non-invaded zone) (Fig. 2B). The reduction of worker abundance was higher in the invaded zone than in the non-invaded zone, and the high differences between zones detected in May (higher abundance in the invaded zone) decreased until August when the abundance in the two zones was similar. This explains the significant interaction zone x month (ANOVA interaction effect:  $F_{3,474} = 5.27$ ,  $P < 0.01$ ). This variation between months was significantly correlated with the temperature and humidity in the invaded zone (Pearson's correlation coefficient: (temperature)  $r = -0.975$ ,  $P < 0.05$ ; (humidity)  $r = 0.985$ ,  $P < 0.05$ ) but not in the non-invaded zone ((temperature)  $r = -0.713$ ,  $P = 0.287$ ; (humidity)  $r = 0.716$ ,  $P = 0.284$ ). The mean ant biomass per 5-minute sample in the invaded zone (0.43 0.04 mg; mean SE) was significantly lower than in the non-invaded zone (1.72 0.18 mg) (ANOVA zone effect:  $F_{1,474} = 49.73$ ,  $P < 0.001$ ) (Fig. 2C). The mean ant biomass varied between sampling months (ANOVA month effect:  $F_{3,474} = 5.91$ ,  $P = 0.001$ ) (Fig. 2C). In the invaded zone the ant biomass decreased progressively through the four months, whereas in the non-invaded zone the ant biomass presented a noteworthy peak in June and decreased in the subsequent months. This peak in June in the non-invaded zone could explain the significant interaction zone x month (ANOVA interaction effect:  $F_{3,474} = 3.00$ ,  $P = 0.030$ ). This variation between months was significantly correlated with



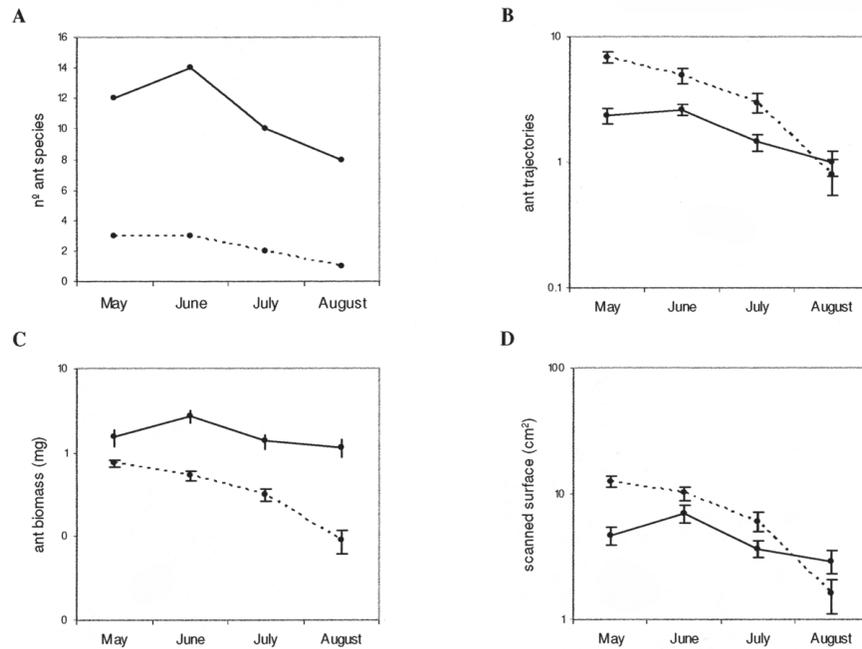


Fig. 2. Number of ant species (A), mean number of ant trajectories (B), mean ant biomass (C) and mean soil surface scanned by ants (D) at the two study zones by the four sampling months. Invaded zone in broken lines and non-invaded zone in solid lines. Error bars indicate standard error of mean. Note log scale in B, C and D.

the temperature and humidity in the invaded zone (Pearson's correlation coefficient: (temperature)  $r = -0.969$ ,  $P < 0.05$ ; (humidity)  $r = 0.980$ ,  $P < 0.05$ ) but not in the non-invaded zone ((temperature)  $r = -0.201$ ,  $P = 0.799$ ; (humidity)  $r = 0.240$ ,  $P = 0.760$ ).

### Soil surface searching

The intensity of soil surface searching done by ants in the invaded zone ( $7.84 \pm 0.63 \text{ cm}^2$ ; mean SE) was significantly higher than in the non-invaded zone ( $4.62 \pm 0.41 \text{ cm}^2$ ) (ANOVA zone effect:  $F_{1,474} = 6.35$ ,  $P < 0.05$ ) (Fig. 2D). The Argentine ant was responsible for 97.25% of the soil searching surface in the invaded zone and its searching ability ( $7.62 \pm 0.63 \text{ cm}^2$ ) was higher than the searching of all the native ants in the non-invaded zone. The estimated time needed by ants for a complete search of a  $10 \times 10 \text{ cm}$  surface was 63.78 minutes in the invaded zone and 108.24 minutes in the non-invaded zone. The intensity of soil surface searching varied between sampling months (ANOVA month effect:  $F_{3,474} = 23.80$ ,  $P < 0.001$ ) decreasing from May to August in the two study zones

(Fig. 2D). However, this reduction in searching intensity was higher in the invaded zone than in the non-invaded zone (where a peak in June was observed), and the high differences between zones observed in May (higher searching in the invaded zone) decreased until August when the inverse was true and searching intensity was higher in the non-invaded zone (ANOVA interaction effect:  $F_{3,474} = 5.19$ ,  $P < 0.01$ ). This variation between months was significantly correlated with the temperature and humidity in the invaded zone (Pearson's correlation coefficient: (temperature)  $r = -0.963$ ,  $P < 0.05$ ; (humidity)  $r = 0.993$ ,  $P < 0.01$ ) but not in the non-invaded zone ((temperature)  $r = -0.369$ ,  $P = 0.631$ ; (humidity)  $r = 0.400$ ,  $P = 0.600$ ).

## DISCUSSION

### **Ant species assemblages and worker abundance**

The well documented decimation of the native ant fauna after the Argentine ant invasion worldwide results again demonstrated in this study. Our results show that the ant diversity was drastically reduced after the Argentine ant invasion. Both the ant species richness and the homogeneity of their abundances were much lower in the invaded zone, which became monopolized by the invasive *L. humile*. Moreover, two of the three native ant species detected in the invaded zone, *Pheidole pallidula* and *Leptothorax racovitzai* (Bondroit), appeared in only one of the 241 samples, so we cannot conclude that they successfully coexisted with the Argentine ant. The third native ant detected in the invaded zone, *Plagiolepis pygmaea* (Latreille), is a cryptic species that seems not to be affected by the invasion as its presence and abundance are similar in the two study zones. The inability of most of the native ant species to coexist with the invasive *L. humile* has been described in other invaded areas (Human & Gordon 1997, Holway 1998a, 1999). Two mechanisms have been proposed to explain the displacement of the native ant fauna caused by the Argentine ant invasion: exploitative competition and interference competition (Human & Gordon 1996, Holway 1999). Our findings (despite being obtained separately in invaded and non-invaded areas and not along the edges of the invasion) concur with the exploitative competition mechanism, as the lower time to scan the soil surface and the higher worker abundance could allow this invasive species a more efficient exploitation of resources through a faster localization and higher worker recruitment to get them.

The direct modification of the ecosystem caused by many invaders has cascading effects for resident biota and these effects can have ramifications throughout the system (Crooks 2002). Thus, the reduction of the assemblage biodiversity of the ant community after the

Argentine ant invasion, which becomes almost completely composed of only *L. humile*, can cause changes in resource exploitation and in the different interactions between ants and other animal and plant species in the ecosystem. Different ecological interactions could be altered after the invasion by an increase, replacement, or decrease of their intensity. Thus, different animal and plant species could be directly or indirectly affected and their survival increased, decreased, or unaltered. Many of these effects have been described for the Argentine ant and for other invasive ant species, and some are compiled by Holway *et al.* (2002a). The level of these changes depends on the ability of the Argentine ant in assuming the role of the displaced native ant species.

#### **Ant assemblages' biomass**

Despite the higher worker abundance observed in the invaded zone, the ant biomass was four times higher in the non-invaded zone. This reduction of the ant biomass after the Argentine ant invasion is explained because most of the native ant species in the non-invaded zone, despite being of little importance numerically, have a higher mass than *L. humile* (which represents 95.9% of the biomass in the invaded zone). This smaller size of the Argentine ant compared with most of the native ant species is common in many of the invasive ant species of the planet (McGlynn 1999b). This result contrasts with those observed by Human and Gordon (1997) and Holway (1998a) who detected an increase and the maintenance respectively of the total ant biomass after the Argentine ant invasion. The opposite of our finding was also documented with other invasive ant species: *Solenopsis invicta* (Porter & Savignano 1990) and *Pheidole megacephala* (Hoffmann *et al.* 1999), whose invasions implied an increase of the total ant biomass.

#### **Soil surface searching and resource exploitation**

If ants "...essentially vacuum the soil surface" (Reichman 1979), this effect is amplified in the Argentine ant invaded areas. The scanning of the soil surface is 1.7 times faster in the invaded zone than in the non-invaded zone. Moreover, we have to take into account that all the ant species detected in the invaded zone presented an antennal gap of less than 3 mm (mean = 1.49 mm), whereas this distance is surpassed by most of the native ants in the non-invaded zone (mean = 3.58 mm). This implies that differences in the searching distances covered by ants are higher (total *L. humile* = 7752.5 cm; total non-invaded zone = 3545 cm) than differences obtained on the searching surface. This can be explained by the higher worker abundance of the Argentine ant in the invaded zone compared with the abundance of all the native ants in the non-invaded zone. Furthermore, the long periods we spent in the field

observing the ant foraging activity allow us to propose another characteristic which could simultaneously enhance the higher soil surface searching ability of the Argentine ant (despite not being experimentally contrasted): a higher speed of displacement of the Argentine ant workers compared with the main species of the non-invaded zone. Hölldobler and Wilson (1990) referred to this characteristic with the term “tempo”. As they described it, some ant species “...literally seethe with rapid motion”, just as we observed in the case of the Argentine ants, in contrast with the species with a low tempo whose workers “...walk slowly and with seeming deliberation”. This character should be directly correlated with rates of resource discovery and thus with exploitative competitive ability (Davidson 1998).

The higher scanning ability of the Argentine ant will alter the level of exploitation of resources after the invasion. This alteration will be different for each resource depending on the requirements of the invading ants compared to the ant assemblages previous to the invasion, each resource being more, less, or similarly exploited. Nonetheless, it is certain that any resource will remain undiscovered on the soil a shorter time in the invaded zone than in the non-invaded zone. That conclusion was reached in a previous study (Gómez & Oliveras 2003) in which the time needed by *L. humile* workers to find seeds randomly placed over the soil surface in an invaded area was three times lower than the time needed by native ants in the non-invaded area. Similar data was used recently (Gibb & Hochuli 2003) to estimate the effect on resource use by ants in habitats with and without the presence of *Iridomyrmex purpureus*, the meat ant. This information represents an indirect measure of the ecosystem resource use.

#### **Abiotic conditions influence**

The mean number of ant trajectories, the mean soil surface searched, and the mean ant biomass varied between months. In the invaded zone these variations were significantly correlated with environmental variations in temperature and humidity, whereas not in the non-invaded zone. This is because the invaded zone is monopolized by the Argentine ant and therefore varies according to single species behavior, whereas in the non-invaded zone the higher number of species and the lower dominance of a single species make its global response less linked to environmental changes. The low levels of the total number of ant species and the total number of functional groups observed in August is explained by the lower activity of ants due to the high temperatures, reducing the probability of detecting some of them.

The correlation of the ant activity with abiotic conditions (such as temperature and humidity) is important because ants characteristically forage within certain temperature ranges, hence competitive interactions between species may be reduced and even avoided depending on environmental factors (Hölldobler & Wilson 1990). In Mediterranean ant communities behaviorally dominant ants have a more limited thermal tolerance than subordinate species (Cerdá *et al.* 1997) and are more heat intolerant (Cros *et al.* 1997). This is because the important daily and seasonal fluctuations of environmental factors (mainly temperature) in the Mediterranean areas periodically reverse the order of competitive superiority among the species, and disrupt the expected transitive hierarchies allowing a greater number of competing species to coexist (Cerdá *et al.* 1997). Our results concur with those observed by Witt and Giliomee (1999) and by Holway *et al.* (2002b) indicating that *Linepithema humile* is more active under warm soil temperature and moist conditions than under hot, dry conditions. Its maximal activity temperature at foraging is lower than many of the Mediterranean Iberian ant species (Cerdá 2001). This explains the decrease of its activity observed from May to August, in direct relation to the increase of the temperature and the decrease of humidity. Consequently, its competitive ability should decrease in hottest months, and is during these periods when the native ant species could offer relative resistance to the advance of the invasion. This concurs with the seasonal variation of the rate of expansion of the Argentine ant detected by Sanders *et al.* (2001) in northern California in accordance with physical environmental changes. Thus, Holway (1998b) and Holway *et al.* (2002b) postulated the necessity of considering variation in the physical environmental conditions and not only the biotic interactions in evaluating the community-level vulnerability to invasion.

#### CONCLUSION

If a numerically dominant species is one that dominates the community abundance and/or biomass (Davidson 1998), then our results could be evidence of the numerical dominance of the Argentine ant in the invaded Iberian Mediterranean areas. This dominance is not explained by a higher ant biomass in comparison with non-invaded zones but by the higher monopolization of the ant abundance and biomass exerted by *L. humile* in the invaded zones. As the invasion progresses, and the native ants become displaced due to their lower exploitative and interference competition ability when faced with *L. humile*, the dominance of resources and community biomass exerted by the Argentine ant becomes more important. The higher competitive

ability of the Argentine ant vs native ants is apparently variable due to the seasonally changing environmental conditions of the Mediterranean climate areas. However, its continuous expansion in these areas indicates that its mean competitive ability for the whole of the year is also higher than natives.

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