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Scavenging in Mediterranean ecosystems: effect of the invasive Argentine ant

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Abstract Above-ground invertebrates may represent a high proportion of animal biomass, but few data are available on their fate after death. In Mediterranean ant communities, they are frequently scavenged by ants. Here, we assessed the consequences of Argentine ant invasion on the removal of arthropod corpses in Doñana National Park (SW Spain). In three natural habitats that differed in their degree of vegetation cover (i.e. protection for ants against high temperatures), we experimentally provided dead *Drosophila*, and observed their disappearance over a 60-min period at different times of day and year. The habitats used were isolated cork oak trees, pine tree forest and dry scrubland; we compared invaded with uninvaded plots in each. Oak trees were the most invaded habitat, while scrubland was the least and the only one where the Argentine ant coexisted with native ant species. In accordance with this degree of invasion, the Argentine ant removed the highest percentage of dead flies in oak trees and the lowest in scrubland. Its performance as scavenger was higher than uninvaded ant communities, but it was reduced at high temperatures, when native species were highly efficient. The saturated distribution of the Argentine ant colony seems to be the key to its efficiency. We discuss how the occurrence and scavenger efficiency of the Argentine ant could affect the nutrient cycling and the progression of its invasion.

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Introduction

Decomposition is a natural process responsible for the return of organic material to the ecosystem. It is estimated that approximately 99% of the organic resources that undergo decomposition in a terrestrial ecosystem are plant-derived or come from faecal matter, while animal carrion might represent, at most, 1% (Carter et al. 2007). Although invertebrates represent a high proportion of the animal biomass, few data are available on the degradation process of invertebrate carcasses in natural ecosystems or the organisms involved in this process (Retana et al. 1991). In addition to impacts that animal biomass can have directly on the cycling of organic materials by decomposition, arthropod carcasses can also provide an important energy and nutrient source for arthropod scavengers (Seastedt and Tate 1981; Seastedt et al. 1981). Arthropod corpses have been shown to

disappear very quickly, confirming the importance of this limited resource for scavengers (Retana et al. 1991).

In many different habitats, the main scavengers of small arthropod corpses are ants as they have some favorable traits such as their numerical advantage or their efficiency as collective foragers (Fellers and Fellers 1982; Fellers 1987; Retana et al. 1991; Cerdá et al. 1998a, 2009). Differences in the removal of arthropods corpses by ants are driven by the availability of other resources, the type of habitat and microhabitat, but also by the established ant community (Saks and Carroll 1980). In Mediterranean ecosystems it has been shown that the structure of ant communities is modulated by the different use of time for foraging by species to avoid interspecific competition, as well as by environmental factors, mainly temperature (Cros et al. 1997). However, Cerdá et al. (1998a) reported that ant communities in different Mediterranean habitats are composed of different scavenger species, with reduced overlap between their foraging activities along the day. The result is that the ant community of each habitat efficiently removes arthropod corpses over the course of a day, in spite of environmental factors.

Particularly dramatic changes in the structure of communities occur when introduced ant species compete with native ones (Sanders et al. 2003; von Aesch and Cherix 2005; Le Breton et al. 2007; Sarty et al. 2007). The Argentine ant, Linepithema humile, is currently considered a widespread and abundant invasive species (Holway 1999). Environmental factors, especially temperature and humidity, are boundaries to their invasion of different habitats, such as between riparian corridors and dry scrublands (Holway 2005). In many parts of the world, the Argentine ant displaces native ants (Cammell et al. 1996; Holway 1998, 1999; Suarez et al. 2001). When it invades, the Argentine ant is aggressive and ecologically dominant, wielding a behavioral and numerical dominance over native ants, and rarely coexisting with them (Suarez et al. 2001). The question arises as to what role the Argentine ant may play in the disappearance of arthropod corpses and nutrient cycling. Depending on the extent to which the Argentine ant is able to co-opt the functional role of native ant species, the implications for the ecosystem may be more or less severe (Crist 2009; Estany-Tigerström et al. 2010).

On the one hand, in its introduced range, the Argentine ant has been shown to feed mainly on honeydew of homoptera, instead of scavenging or predating invertebrates as do most native ant species (Tillberg et al. 2007). Consequently, in invaded communities from which native scavengers have been excluded, carcasses could remain in the litter and be recycled into the soil through decomposition. On the other hand, the structure of colonies of the invasive Argentine ant relies on its huge numbers and their exceptional social organization (Giraud et al. 2002; Heller et al. 2008), resulting in a relatively high local abundance in comparison to native species (Cammell et al. 1996). As a result of their high numbers, the scavenging potential of Argentine ants could be significant in relation to that of native ants.

Here we try to assess the consequences of Argentine ant invasion in the removal of arthropod corpses in three natural habitats that differ in their degree of vegetation cover—cork oak trees, pine tree forest and scrubland—of Doñana National Park. The invasion of the Argentine ant at Doñana Biological Reserve is limited to houses and to some natural habitats such as cork oak trees and pine tree forests but occurs mostly near disturbed habitats such as main trails, concrete walls, or wells (Carpintero et al. 2003, 2005; Angulo et al. 2007). First, we looked at the degree of invasion across the three habitats selected and the structure of the ant community therein. Second, we examined whether the Argentine ant is more or less effective at removing dead arthropods than native species, and if this is modulated by the degree of invasion in each habitat or environmental conditions. Finally, we discuss the implications of Argentine ant invasion on the decomposition of dead arthropods and the soil nutrient cycle.

Materials and methods

Study area

The study was performed from May to October 2009 in the Doñana Biological Reserve of the Doñana National Park (37°1′N, 6°33′W; Huelva, SW Spain), 5 km away from the coastline. Located in the mouths of the Guadalquivir and Guadiamar rivers, its main ecosystems are the marshland, the coastal dunes, and the scrubland, which includes some scattered pine

Fig. 1 a Aerial view of the study area (Doñana Biological Reserve, SW Spain) showing sampling plot situation (*UNI* uninvaded; *INV* invaded by the Argentine ant) in cork oak trees, scrubland and pine tree forest. **b** Daily curves of mean temperatures for each habitat and season. *Grey bars* show the three different sampling periods of the day (morning, midday, evening)
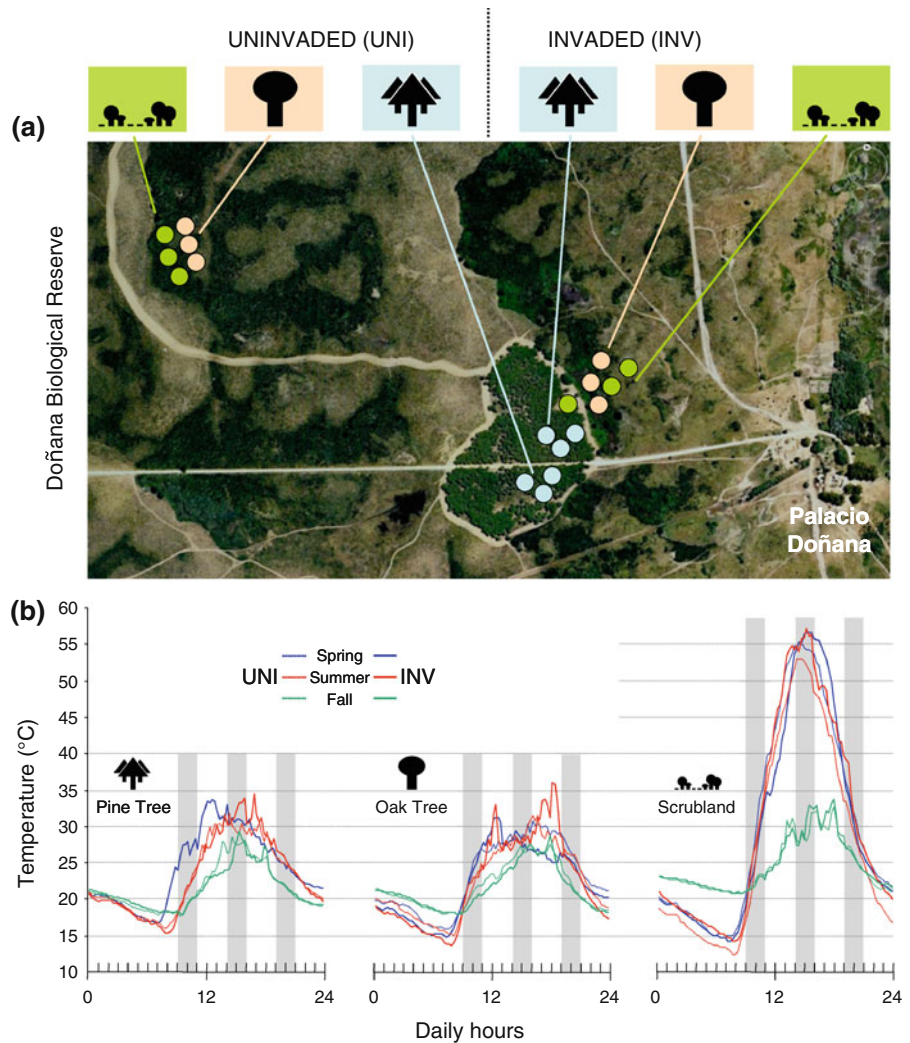
tree forest (*Pinus pinea*), savine trees (*Juniperus sabina*) and isolated cork oak trees (*Quercus suber*). The Doñana Biological Reserve is inhabited by more than 30 ant species; the Argentine ant is the only invasive species (Carpintero et al. 2003). The Argentine ant was already found in the reserve's field station (El Palacio) in the 1970s but it was not found in cork oak trees at this time (José Boixo, pers. comm.).

Our study site, in the surroundings of the Pinar de San Agustín, is around 1 km from El Palacio, along the main trail that leads from the entrance of the reserve (Fig. 1). At this site, we conducted field experiments in three different habitats: dry scrubland ('monte blanco'), cork oak trees, and pine tree forest. In each of the habitats, six plots were established; three were invaded by the Argentine ant and three

were uninvaded. Scrubland invaded by the Argentine ant was paired with invaded cork oak habitat; scrubland plots were established in proximity to the invaded cork oak trees. The same pairing was performed between uninvaded cork oak trees and scrubland (Fig. 1). Our choice of study sites was somewhat limited for two reasons. First, access to some of the most invaded areas is prohibited during some periods of the year because of conservation concerns (e.g. Las Pajareras, which is home to a nest of the Spanish imperial eagle). Second, the Argentine ant has a particular distribution pattern in Doñana, likely resulting from its pattern of introduction and invasion, and it was thus impossible to find an area in which the three main natural habitats (invaded or uninvaded) were spatially interspersed.

To characterize the abiotic conditions of each habitat, temperature was recorded every 15 min with a HOBO data-logger. One HOBO 4-channel external logger with four external temperature sensors measuring ground surface temperature was installed in each one of following plots: two invaded and two uninvaded cork oak trees (on the ground under the canopy of each tree), two invaded and two uninvaded scrubland plots, and one invaded and one uninvaded pine tree plot.

Occurrence of ant species and removal of arthropod corpses

In each plot, a transect of 15 m was established and 20 dead *Drosophila melanogaster* were placed along the transect. Each fly was placed in a plastic white spoon so its presence or absence could easily be detected. Over the course of 60 min, the removal of corpses was surveyed at the following time points: 1, 3, 5, 15, 20, 25, 30 and 60. Temperatures were recorded with an Extech mini IR thermometer® (resolution 1°C) at the beginning and end of each transect at minutes 1 and 60. To determine ant species presence in each plot, we placed 4 pitfall traps (200 ml. PVC cups 2/3 full of water and soap) along the transect (corresponding to 0, 4, 8 and 12 m along the transect), which were open during the 60-min period of observation. Pitfall traps were placed at least 1 meter away from axis of the transect, to limit possible interferences with ants collecting dead flies. Experiments were repeated at three different times of the day: in the morning (9.00–11.00 h LST), at midday (13.00–15.00 h) and in the evening (19.00–21.00 h) and in three different seasons: spring, summer and fall.

The occurrence of ant species was calculated from the presence of ant species in the pitfall traps. It refers to the time in which the experiment was done; pitfall traps were open 1 h during each period of the day (total 3 h per day), in order to include the different diurnal activity patterns of ant species in the area.

We also used the total number of workers of each species caught in pitfall traps (summed over the 3 h of trapping) in each plot to calculate a comparative mean biomass for each habitat and season. Mean species weight was obtained from dry weight of 10–30 individuals. Although pitfall traps are not the best method to assess biomass, they provide an acceptable approximation if comparing plots across habitats and seasons (Bestelmeyer and Rios Casanova 2010).

In order to assess which species (ants or not) removed the prey, we performed focal observations on five more spoons per transect, during the last 30 min of the 60-min survey of prey disappearance. This protocol allowed us also to verify that all scavenger ant species could climb onto the spoons. In total we placed 810 dead flies (corresponding to 15 spoons per habitat, in three habitats, three seasons, two Argentine treatments and 3 times of the day).

Data analysis

First, to ascertain the degree and impact of invasion, we determined if ant occurrence varied in the different habitats, in invaded and uninvaded plots, or across all seasons. We define the occurrence of a given ant species as the sum of pitfall traps containing this species in each plot along the daily surveys (3 surveys per day for each plot). The dependent variable was the occurrence of all ants (the sum of the occurrences of each ant species) and the three main factors were invasion status, habitat type, and season; thus the corresponding sample size of this analysis was N = 54 (three transect per habitat, three habitat, three seasons and two levels of invasion). We performed a stepwise backward regression starting from a fully saturated model (containing all possible interactions). Due to the characteristics of the dependent variable, we used a generalized linear model with binomial distribution and logit link function (proc. GENMOD, SAS 9.1, SAS Inst. Inc. 2008). Tukey HSD post-hoc tests were performed to know which groups significantly differ from others.

To know if the degree of invasion was affected by the temperature, we used a generalized linear model with binomial distribution and logit link function to determine if the temperature measured during our surveys significantly predicted Argentine ant occurrence. Data of each transect in each habitat and each season in invaded plots were treated independently in this analysis (N = 27).

To test for differences in the removal of dead flies between invaded and uninvaded habitats, we used survival analysis, which can estimate the effect of different factors and covariates on the time-to-event data. In all survival analyses, maximum sample size

correspond to each fly (each spoon), at each moment of the day, each transect, each habitat, each season and each invasion status (N = 3240) and could be reduced in relation to the factors included or not. First, we compared the removal of dead flies between invaded and uninvaded plots using the Cox's F test for comparing two samples. Second, we examined the effects of the temperature (measured during our surveys) on fly removal within invaded and uninvaded plots using a Cox proportional hazards regression. In this analysis, we considered each transect individually (at each time of the day, in each habitat and season). We also tested the effect of the time of the day (morning, midday and evening) on fly removal, using an independent multiple sample test. In this multiple sample test, the transects were pooled by the time of the day (morning, midday and evening), without taking into account habitat or season. We also tested the relationship between temperature and time period using an analysis of variance (ANOVA). Third, we tested the effects of habitat type and season on fly removal within invaded and uninvaded plots performing independent multiple sample tests for each variable. These analyses were performed in STATISTICA 8.0 (StatSoft Inc. 2007).

Results

Occurrence of ant species

We tested for differences in the occurrence of ants among the studied habitats and across seasons to ascertain the degree of invasion. The final model of the stepwise backward regression ($R^2 = 75.3\%$) found significant effect for invasion status, habitat type, and season on the occurrence of ant species ($\chi^2 = 199.54$, $P = < 0.001$; $\chi^2 = 50.38$, $P = < 0.001$; $\chi^2 = 27.58$, $P = < 0.001$, for the invasion, the habitat and the season respectively, N = 54). Moreover, the interaction between invasion status and habitat type as well as the interaction between habitat type and season were also significant ($\chi^2 = 22.18$, $P = < 0.001$; $\chi^2 = 32.57$, $P = < 0.001$, for each interaction respectively, N = 54, Fig. 2).

The significance of the first interaction between invasion status and habitat type was the most interesting, showing that the overall occurrence of ants was similar among uninvaded habitats and was
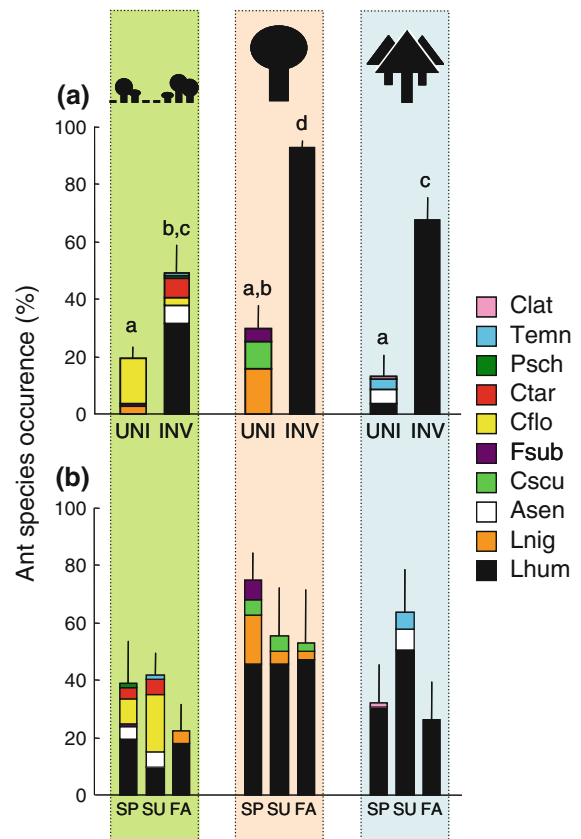
Fig. 2 Mean (+SE) occurrence of ant species in scrubland, cork oak trees and pine tree forest. **a** Effects of the invasion and the type of habitat (codes and symbols as in Fig. 1); groups that were not significantly different based on Tukey post-hoc test share a common letter. **b** Effects of the type of habitat and season (*SP* spring; *SU* summer; *FA* fall). Ant species abbreviations: *Clat Camponotus lateralis*; *Temn Temnothorax* sp.; *Psch Plagiolepis schmitzii*; *Cflo Cataglyphis floricola* (black morph); *Ctar Cataglyphis tartessica* (formerly *C. floricola* orange morph); *Fsub Formica subrufa*; *Cscu Crematogaster scutellaris*; *Asen Aphaenogaster senilis*; *Lgra Lasius grandis*; *Lhum Linepithema humile* (Argentine ant)

significantly lower than in invaded habitats (Fig. 2a). However, the invaded habitats significantly differed from each other: the highest ant occurrences were found in the oak trees, followed by the pine tree forest, while the scrubland had the lowest ant occurrences (and which were not significantly different from those in the uninvaded oak trees). We can also see that, in uninvaded plots, all the species detected were native and thus the overall occurrence corresponded to the native ant community (Fig. 2). In contrast, in the invaded plots, the Argentine ant was

the only species that we detected in the oak trees and in the pine tree forest, so the overall occurrence in those habitats corresponded to the invasive species (92.6 and 67.6%, respectively). However, in the scrubland, the Argentine ant coexisted with the most thermophilic species of the native ant community, confirming the high temperature profiles of this habitat (Fig. 1). In fact, the mean occurrence of native ants in the scrubland was similar in invaded and uninvaded habitats (17.6 and 19.4%, respectively).

The interaction between the habitat type and the season resulted from particularly high ant occurrences in the oak trees in the spring (Fig. 2b). The Argentine ant was present over all seasons with increased abundance in the oak trees and pine forest.

In general, relative ant biomass was higher in invaded than in uninvaded plots, except in summer, when scrubland and pine tree forest demonstrated similar values whether invaded or uninvaded (Table 1).

Finally, the occurrence of Argentine ants was negatively related to the averaged temperatures recorded during the surveys ($\chi^2 = 33.11$, $P < 0.001$, N = 27).

Removal of dead flies

Removal of dead flies was almost exclusively performed by ants: a total of 352 flies were removed (43.46%), from which 349 were removed by ant species (99.14%). Only in three cases (0.86%) was a beetle (*Pimelia* sp.) seen to remove the fly. These three cases took place in the scrubland, once in an invaded habitat and twice in uninvaded habitat.

The time to removal of dead flies was significantly different between invaded and uninvaded plots (F = 3.31, $P < 0.001$, N = 3239). Specifically, we

Table 1 Relative ant biomass [mg, mean (SD)] for each habitat, invaded or not (Inv), and each season

Inv	Season	Cork oak tree	Pine tree forest	Scrubland
Yes	Spring	8.3 (7.3)	12.8 (6.6)	6.6 (7.4)
	Summer	24.0 (20.2)	7.0 (0.6)	2.4 (0.9)
	Fall	11.6 (8.6)	1.6 (1)	2.6 (3.6)
No	Spring	6.9 (4)	0.2 (0.3)	2.1 (2.7)
	Summer	1.5 (0.3)	7.5 (5.3)	4.2 (3.3)
	Fall	0.6 (0.5)	0.0	0.3 (0.3)

found that the percentage of flies removed in the invaded plots in 60 min was very high compared to in the uninvaded plots (70.2% compared to 30.6%).

We found a significant effect of temperature on fly removal in both invaded and uninvaded plots ($\chi^2 = 45.21$, $P < 0.001$, N = 1619; $\chi^2 = 323.03$, $P < 0.001$, N = 1620, for invaded and uninvaded plots respectively). However, temperature had a different effect in invaded versus uninvaded plots. On invaded transects, higher temperatures corresponded to a decrease in the percentage of flies removed; on uninvaded transects, higher temperatures corresponded to an increase in the percentage of flies removed.

When testing the effects of the time of day on fly removal in invaded plots, we obtained a different pattern: removal was similar in invaded plots across time periods ($\chi^2 = 0.39$, $P = 0.82$, N = 1619) even though mean temperatures were significantly different at different times of day in these invaded plots (26.3, 34.3 and 24.6°C in the morning, midday and evening respectively; F = 311.96, $P < 0.001$). This pattern could result from the fact that, in the cork oak trees and pine tree forest, the Argentine ant is the only species removing flies while, in the scrubland, there are also some native species collecting flies. In fact, the finding that higher temperatures correspond to a decrease in removal on invaded transects can be observed in cork oak trees and pine tree forest but not in scrubland if we separate transects by the time of day (Table 2).

In uninvaded plots, there were significant differences in fly disappearance among time periods ($\chi^2 = 62.68$, $P < 0.001$, N = 1620). Removal of flies was very slow in the morning, very fast at midday, and slow in the evening. In this case, the pattern corresponded to differences in the mean temperatures of the time periods in which experiments were performed (F = 249.06, $P < 0.001$), with the highest temperatures at midday (37.3°C) differing significantly from the morning and evening temperatures (27.6 and 27.4°C, respectively).

The season and habitat type also affected fly removal in invaded and uninvaded plots ($\chi^2 = 62.28$, $P < 0.001$, N = 1619; $\chi^2 = 132.94$, $P < 0.001$, N = 1620, for the season in invaded and uninvaded plots respectively; and $\chi^2 = 436.28$, $P < 0.001$, N = 1619; $\chi^2 = 152.36$, $P < 0.001$, N = 1620, for the habitat type in invaded and uninvaded plots respectively). In general, fly removal was always

Table 2 Prey removed (%) and corresponding temperatures (°C, Temp) for each habitat, invaded or not (Inv), during each time of the day for the summer period [means (SD)]

Inv	Time of the day	Cork oak tree		Pine tree forest		Scrubland	
		Temp	%	Temp	%	Temp	%
Yes	Morning	18.4 (1.5)	98.3 (2.9)	28.3 (2)	93.3 (7.6)	27.3 (5.2)	45 (32.8)
	Midday	22.4 (1.6)	96.7 (5.8)	33.3 (1.8)	83.3 (20.8)	52.4 (0.8)	73.3 (20.2)
	Evening	20.1 (0.9)	100 (0)	26.1 (0.1)	96.7 (2.9)	21.3 (1.6)	35 (18)
No	Morning	24.3 (1.5)	20 (13.2)	23.4 (0.4)	6.7 (2.9)	33.1 (2.7)	6.7 (11.5)
	Midday	30.4 (1.2)	46.7 (10.4)	34.7 (1.4)	11.7 (10.4)	57 (1.7)	96.7 (2.9)
	Evening	26.5 (0.7)	43.3 (7.6)	27 (0.4)	25 (5)	30 (1.5)	26.7 (16.1)

faster in invaded plots that in uninvaded plots, for all seasons and habitat types. However, disappearance trends across seasons were inverted for uninvaded versus invaded plots (Fig. 3). In uninvaded plots, flies were removed most quickly in the spring, followed by the summer and the fall; in invaded plots, removal was slowest in the spring and quickest in the summer (Fig. 3a). Removal time also varied by habitat type in invaded and uninvaded habitats. In uninvaded plots, flies were removed most quickly from the scrubland, followed by the oak trees and the pine tree forest; in

invaded plots, removal was slowest in the scrubland and quickest in the oak trees (Fig. 3b).

This variation in the trends seen in the different habitats for invaded and uninvaded is also observed within seasons. For example, if we compare the removal curves in summer, trends of each habitat were inversed between invaded and uninvaded habitats, (Fig. 4c, d). In spring, the trend was similar to the summer, but with a higher variability of fly disappearances during the day, especially in the uninvaded scrubland (Fig. 4a, b). In fall we can also observe some inversion in the removal curves between invaded and uninvaded habitats, but there is a severe reduction in the removal of dead flies in uninvaded habitats (Fig. 4e, f).

There was also significant variability in the percentage of flies that disappeared (at min 60) during different times of day (Fig. 4). In the summer, daily variability in the invaded oak tree habitat was very low relative to that in uninvaded oak trees, while daily variability in invaded pine tree forest was higher than in uninvaded pine tree forest (Fig. 4c, d). It is clear that the daily variability in scrubland was higher than in the other habitats in spite of the invasion by Argentine ant, except in the fall in uninvaded plots. Daily variability in fly removal could probably be linked to daily temperatures in each habitat and season. Temperatures during the day were similar in oak trees and pine tree forest for all seasons and were similar as well to those in the scrubland in fall (Fig. 1); however, the scrubland had very high midday temperatures in spring and summer. This pronounced variability in spring and summer daytime temperatures could explain the higher daily variability in fly removal in the scrubland during these seasons.
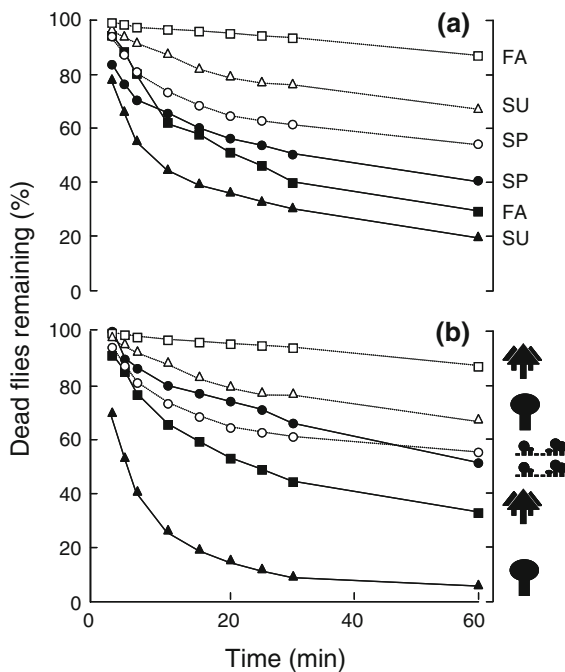
Fig. 3 Effects of **a** invasion and season and **b** invasion and habitat, on the percentage of dead flies remaining along time. Open forms represent uninvaded habitats while filled forms represent the invaded ones (codes and symbols as in Fig. 2)
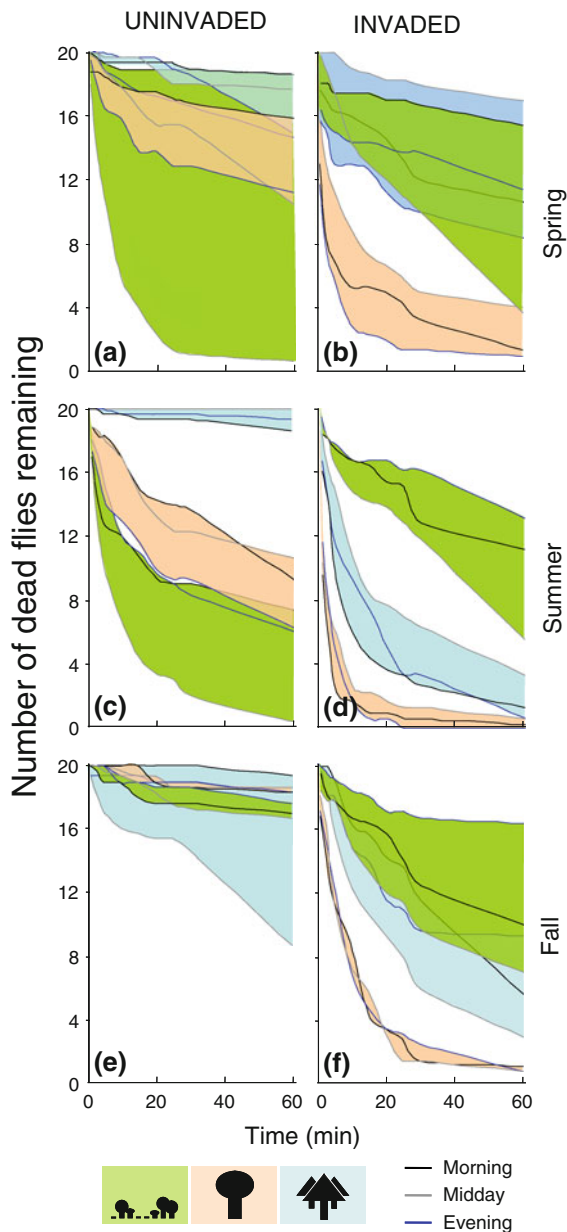
Fig. 4 Dynamics of dead flies disappearance along time in the different habitats (invaded or not) and different seasons (codes and symbols as in Fig. 1). Morning, midday and evening disappearance curves (mean values) are shown and the surfaces represent the range of observations along the day for each habitat

Discussion

In this study, we explored the consequences of Argentine ant invasion on the removal of arthropod corpses in three Mediterranean habitats. First, we

showed that the degree of invasion varies among habitats and appears to be related to the degree of vegetation cover present, which provides protection against high temperature for ants. The most invaded habitat was cork oak trees followed by the pine tree forest, while the scrubland was the least invaded and the only one in which we found that the Argentine ant coexisted with native species. The native species present there were among the most thermophilic. Second, we found that the Argentine ant removed more flies more quickly than native ant species found in uninvaded communities. The speed of removal depended on habitat type and season and could be linked: (1) to the occurrence of Argentine ants in each habitat, which had a higher occurrence than all of the native ants in uninvaded habitats, and (2) to the limiting effect of temperature on Argentine foraging activity. Even if native species were efficient foragers at high temperatures, their scattered spatial distribution is perhaps less effective than that of the Argentine ant, whose colonies are formed by groups of interconnected nests spread along a wide surface (Heller et al. 2008). We can conclude that when the Argentine ant invades, its ability to exclude native species depends on habitat and temperature. Furthermore, the Argentine ant, which was previously found to feed mainly on Homoptera-honeydew in its introduced range (Tillberg et al. 2007), does collect dead insects in Doñana and, in fact, can be a more effective scavenger than native ants.

Habitat differences of invasion

Holway (1999) showed that the displacement of native ant species by the Argentine ant, by means of exploitative and/or interference competition, is severe in Mediterranean ant communities. All the native species found during our surveys were scavengers. The Argentine ant appeared to successfully exclude all native ants from the oak trees and pine forest but not the scrubland habitats. Although our sampling did not cover 24 h and thus our interpretation can only take into account the time periods sampled, previous studies on the area support our results, confirming that in invaded cork oak trees the Argentine ant excludes all other ant species (Carpintero et al. 2005). Moreover, pitfall trapping over three consecutive days in July and October 2009 showed that no other ant species was present in these invaded trees (unpublished data).

The exclusion of native species from the pine tree forest was an expected outcome of an Argentine ant invasion. Notwithstanding, Way et al. (1997) found in Portugal that *L. humile* failed to spread from a pine plantation to an immediately adjoining cork oak plantation, probably because it was insufficiently abundant to dislodge the large native ant populations in cork oak. In Doñana, however, Argentine ant occurrence was higher in the oak trees than in the pine tree forest. This could be explained by food availability, presumably more limited in the pine tree forest, or by abiotic factors limiting the activity of the Argentine ant, such as temperature or humidity. Since we found that temperature patterns were similar between both habitats in all seasons, this can be rejected as a potential explanation. However, we did not measure the soil humidity, which probably differs between oak trees and pine tree forest due to the more open understory structure in the pine tree habitat and the more closed structure of the oak trees, which frequently have a temporary pond nearby. These differences in humidity likely contribute to differences in invasion potential between these two habitats, as other authors have demonstrated in other Mediterranean ecosystems (Menke et al. 2007).

Oak trees suffered the highest degree of invasion. The total exclusion of native ants in oak trees could be related to the structure of Argentine ant colonies. Heller et al. (2008) showed that spatial area exploited by a colony during the spring or summer was around 400 m^2, consisting of group of nests in which foragers shared food at distances of around 20–30 m. The canopy of individual oaks at our study site covered around 10–15 m of diameter so we suggest that each oak tree had a unique colony that completely saturated the invaded tree.

The structure of the Argentine ant colonies in the scrubland is difficult to infer without more research: is it linked to the colony of the nearest oak tree or is it a colony occupying the scrubland? How are native ants able to be present in the presence of Argentine ants? The low invasibility of the scrubland could be linked to the availability of food resources: woody habitats, such as cork oak trees or pine tree forest, can provide food sources that are scarce in the scrubland, such as tree-living Hemiptera populations (Heller and Gordon 2006; Carpintero et al. 2007). A more likely explanation is temperature regimes and associated environmental humidity. During our surveys, surface daily temperature ranged between 20 and 45.5°C. The Argentine ant occurred at all of these temperatures (as already showed by Carpintero et al. 2007) but its occurrence was higher at lower temperatures. Human and Gordon (1996) showed that, along edges of invasion, the presence of the Argentine ant significantly reduced the foraging efficiency of native ants, and vice versa. Here, we have showed that, although the occurrence of Argentine ant is reduced in the scrubland, the occurrence of native ants in the scrubland was nonetheless similar in invaded and uninvaded habitats (17.6 and 19.4%, respectively). While Human and Gordon (1996) explained those reductions by foraging interferences between native and invasive species, we have shown here that the occurrence of Argentine ant and its efficiency in removing dead flies is negatively related with temperatures, which were higher in the scrubland than in the other habitats. Different thermal requirements may explain the limited invasion of scrubland habitat. The critical thermal maximum and maximal foraging temperature of Argentine ants were significantly lower (40 and 20°C, respectively) than those of common native ants inhabiting the scrubland (50 and 44°C, respectively for *Cataglyphis floricola*, or 46 and 35°C, respectively for *Aphaenogaster senilis*; Cerdá 2001; Angulo et al. 2007). Moreover, the outcome of aggressive interactions at baits also depends on the temperature: *A. senilis* and *C. floricola* win the interactions at higher temperatures (43.0°C) than the Argentine ant (30.3°C) (Angulo et al. 2007).

To spread or not to spread in Doñana?

Given the differences in occurrence and activity of Argentine ant across Doñana habitats, we are interested in the following question: If temperature is a barrier in the scrubland for the Argentine ant, how has it spread to isolated oak trees? The Argentine ant has a low capacity to spread given its unwinged queens and the workers low traveling distances (Heller et al. 2008), smaller than between oak trees. However, we found that the scrubland had similar temperatures to the other habitats in the fall, a temperature window (very likely associated with an increase in soil humidity) that the Argentine ant could exploit to traverse otherwise inhospitable habitat. In fact, we found the Argentine ants in the pitfall traps farther from the invaded oak trees in the fall as

compared to in spring and summer. However, other research has shown that fall might not be the best season for the Argentine ant to spread, as colonies in California tended to be spread across a smaller surface in fall (Heller et al. 2008).

The close association of the Argentine ant to oak trees combined with inhospitable temperatures and probable lack of moisture of the scrubland suggests that the invasion of new trees may be limited by the distances between trees. This suggestion was also made by Heller and Gordon (2006), although the spatial distribution of woody plants in their study site did not appear as scattered as the trees in the scrubland of Doñana. Other factors should also be considered, namely the effect of human activity around houses, roads, trails, and other sites of activity. It is also possible that scavenger raptors nesting in trees, such as black kites (*Milvus migrans*), could transport vertebrate carrion infested by Argentine ant to oak trees (Carpintero et al. 2005). Heller and Gordon (2006) also showed rates of spread of the Argentine ant from the invasion front, while in Doñana the Argentine ant is scattered distributed around houses and other human constructions and oak trees (Carpintero et al. 2003, 2005; Angulo et al. 2007), so it would be difficult to determine a front of invasion. Human and Gordon (1996) showed how the mechanism of the Argentine ant to maintain the invasion was based in the prevention of the establishment of new colonies of native species by preying upon native ant queens. We have also seen heavy predation by the Argentine ant of mated queens of the arboreal native species *Crematogaster scutellaris* arriving to invaded oak trees after nuptial flights (personal observations).

Scavenger activity and the recycling of arthropod corpses

Apart from displacing native ants, Argentine ants may disrupt communities in other ways as well, such as in the recycling of arthropod corpses. Foraging in Mediterranean native ant communities is partitioned in time, with species activity corresponding to their temperature requirements (Cros et al. 1997; Cerdá et al. 1998b). Consequently, daily and seasonal removal of arthropods in the different habitats should depend on the occurrence of scavengers (Cerdá et al. 1998a). The ants found in this study were primarily scavengers. Our results show that the scavenging activity of native ants varies throughout the year. In spring, there is a high degree of daily variability in scavenging, especially in the scrubland, which shifts to more constant level of removal during summer and declines in fall. However, average rates of removal of dead flies by native ants were lower than those obtained by Retana et al. (1991) in a Mediterranean grassland. We did find, however, that the most rapid rates of removal occurred at midday in the scrubland, when the scavenger ant, *Cataglyphis floricola*, was at its peak of activity (Angulo et al. 2007).

In contrast, the scavenging activity of the Argentine ant was both higher and more constant regardless of the season, with a mean scavenging activity over 50% in 1 h (lower in spring, increasing in summer and decreasing a bit in fall, Figs. 3a, 4a), which corresponds to the findings of Carpintero et al. (2007). The high rates of fly removal were also significant in the two most heavily invaded habitats, the cork oak trees and pine tree forests (Fig. 3b). When taking into account both habitat and season, the Argentine ant had higher rates of dead arthropod removal than native ants in our study sites.

In addition to temperature and moisture, and indirectly season, the occurrence and biomass of Argentine ants plays also an important role in explaining the disappearance of dead arthropods. In general, ant occurrence and biomass was higher in invaded than uninvaded areas. Indeed, the effectiveness of Argentine ant in removing invertebrates in invaded environments, such as oak trees and pine tree forests, could be linked to their colony structure; their colonies are formed by groups of interconnected nests. This structure, along with their large colony sizes and/or high nest densities that allow them to cover larger surface areas (Human and Gordon 1996; Heller et al. 2008), contrasts strongly with the scattered, low-density distribution of the native species. This is confirmed by the higher occurrence and biomass of Argentine ant in the most preferred invaded habitats in comparison with the native ant occurrence and biomass in uninvaded habitats.

Ants are important components of ecosystems not only because they constitute a significant proportion of animal biomass but also because they may have impacts on below ground processes by changing nutrient cycling (Crist 2009). The importance of invertebrate decomposition in the cycling of nutrients

may not be as obvious as those of plant litter or vertebrate carrion, even when taking into account the cumulative effect of their higher abundance (Seastedt and Tate 1981; Parmenter and MacMahon 2009). Even if Argentine ants strongly affected the presence and distribution of dead soil invertebrates via the exclusion of native ant species, who are the typical scavengers in this ecosystem, the fact that Argentine ants efficiently remove arthropod corpses suggests that they are essentially co-opting the role of native species. Consequently, their presence might not negatively affect nutrient cycling in these ecosystems. Moreover, given the large sizes and biomass of Argentine ant colonies, the biomass entering into the ecosystem from Argentine ant mortality will likely compensate, if not exceed, the arthropod biomass the Argentine ant retrieves. Finally, as the nutrients and energy of dead arthropods are monopolized by the Argentine ant in invaded habitats, we can suggest that their competitive superiority at scavenging will benefit their colonies and contribute to the progression of their invasion.

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