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## ORIGINAL PAPER

# Humans and scavenging raptors facilitate Argentine ant invasion in Doñana National Park: no counter-effect of biotic resistance

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**Abstract** Biotic resistance by native communities could have a role in the spread of invasive species. This seems to be the case in the invasion of the Argentine ant, *Linepithema humile*, but only when the environment is unfavorable for the survival of the invader. We studied the progress of Argentine ant invasion through favorable and unfavorable habitats of Doñana National Park across three temporal snapshots covering three decades (1992, 2000, 2016). We assessed biotic resistance of the native community using species richness, as well as dominance and community structure. We also explored the role of abiotic factors (quality of surrounding habitat and spatial variables) and of potential vectors of Argentine ant dispersal across unfavorable areas. We found no evidence of biotic resistance after examining native ant species richness, proportion of native dominant ants, or community structure. On the contrary, invasion proceeded from trees with higher ant species

richness, probably because those trees are larger and provide more resources and better protection from aridity. Furthermore, we found evidence that the invasion of new trees across a matrix of unfavorable habitat could be influenced not only by humans, but also by scavenging avian predators, which could act as vectors of ant dispersal through transport of carrion also exploited by the ants. Such leapfrog expansion through mobile predators could represent an overlooked mechanism that would enrich our understanding of invasion dynamics and provide potential opportunities for management of invasive species.

**Keywords** Biotic resistance · Dominance hierarchies · Community structure · Dispersal by mobile predators · *Linepithema humile* · Raptors

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## Introduction

Biological invasions are a well-known worldwide threat to biodiversity, reducing or even replacing native species (Sax and Gaines 2003; Simberloff et al. 2013; Kumschick et al. 2015; Li et al. 2016). Different hypotheses can explain the success, spread, and impact of invaders, like propagule pressure, enemy release, biotic resistance or invasion meltdown hypothesis, among others (Catford et al. 2009; Ricciardi et al. 2013; Heger and Jeschke 2014; Jeschke

2014). Ecosystems can be more resistant to invaders due to either abiotic factors, like environmental tolerance to temperature or moisture (Shea and Chesson 2002; Blackburn et al. 2011), or biotic factors, like food resources or natural predators and competitors (Shea and Chesson 2002; Kumschick et al. 2015). According to biotic resistance theory (Elton 1958), native communities with higher species richness should be less susceptible to invasion by exotic species than ecosystems with fewer component species. In this context, interspecific interactions can act as biotic barriers and prevent a new species from persisting in a highly competitive environment (Holway 1999; Parr 2008; Blight et al. 2014).

Ant communities are good models for testing the relative roles of biotic resistance in the spread of invasive species. Competition in ant communities is important in shaping community structure (Parr 2008; Arnan et al. 2012; Cerdá et al. 2013). Moreover, ants' unique life history traits (e.g. social structure, colony foundation, worker polymorphism) make the study of their movements, invasion dynamics and interactions with the native community interesting (Bertelsmeier et al. 2015, 2017). In addition, invasive ants are among the worst world invaders (Lowe et al. 2000), so understanding the role of biotic resistance is important for future management and prevention of its spread. Hölldobler and Wilson (1990) defined two main types of competition in ants. Exploitative competition refers to the ability of ants to rapidly detect a food resource and recruit a large amount of individuals to exploit it. Interference competition refers to the ability of ants to dominate a food resource through aggression. On the basis of these interactions, ant species have been classified mainly as dominant or subordinate (Vepsäläinen and Pisarski 1982; Savolainen et al. 1989; Arnan et al. 2012, 2017). Dominant species typically shape the species composition of ant assemblages (Cerdá et al. 2013), while subordinate species avoid contact with other species (Arnan et al. 2011). The latter strategy of avoidance allows subordinate species to coexist (Calcaterra et al. 2016). As a result, high rates of dominant species are not inversely proportional to species richness (Arnan et al. 2011).

The Argentine ant, *Linepithema humile*, is an example of a highly dominant ant (Human and Gordon 1996). It is also a highly invasive species, native to South America, which has successfully established around the globe (Lowe et al. 2000; Suarez et al.

2001). This ant possesses life history traits that make it an exceptionally good invader (Table 1; Arnan et al. 2012; 2017). It is unicolonial (individuals move freely among physically separate nests without showing any kind of intraspecific aggression; Holway et al. 1998; Giraud et al. 2002); its colonies are polygynous (elevated number of reproductive females; Hölldobler and Wilson 1977; Passera 1994) and polydomous (single colonies are divided in multiple physical nests; Pedersen et al. 2006; Heller et al. 2008); and it is highly aggressive toward other ant species through both physical and chemical attacks (Suarez et al. 1999; Welzel et al. 2018). When it colonizes a new area, the Argentine ant usually displaces the native ant community and produces a cascade of negative impacts on other taxa including arthropods, small vertebrates, and plants (Holway et al. 2002; Sanders et al. 2003; Rowles and O'Dowd 2009; Alvarez-Blanco et al. 2017). *Linepithema humile* has an overall generalized diet including insects, carrion or nectar (Holway et al. 2002; Angulo et al. 2011), and it has been shown that carbohydrate-rich diets provided by aphids favor its success (Rowles and Silverman 2009). The only aspect of this species' natural history that may constrain its colonization potential is the lack of winged queens, which can prevent dispersal across patches of unfavorable habitat (Way et al. 1997; Holway 1998).

Previous work has demonstrated that native ant communities do not show biotic resistance against Argentine ant invasion when abiotic conditions are favorable for the Argentine ant (Way et al. 1997; Holway 1998; Menke et al. 2007; Rowles and O'Dowd 2007; Roura-Pascual et al. 2011). On the other hand, some dominant native species are capable of resisting the invader Argentine ant. For example, species like *Lasius grandis*, *Tapinoma nigerrimum* or *Iridomyrmex rufoniger* can repel the invader when its propagule size is not adequate (Way et al. 1997; Walters and Mackay 2005; Wetterer et al. 2006; Blight et al. 2010), while some other species like *Crematogaster scutellaris*, *Pheidole pallidula* and *Tetramorium forte* can prevent its spread in habitats that are suboptimal for the Argentine ant (Way et al. 1997).

The Argentine ant expansion has mainly affected areas with a Mediterranean climate but can also be limited by abiotic factors, especially temperature and moisture (Carpintero and Reyes-López 2008; Roura-Pascual et al. 2009, 2011). Although localized

**Table 1** Ant species present in the cork oak trees of the study area in 1992 and in 2016, and their life-history traits

Species	%		Life history traits				
	1992	2016	Dom	Queen	Nest	Forage	Diet
<i>Linepithema humile</i>	–	–	1	1	1	1	0, 1
<i>Crematogaster scutellaris</i>	76	84	1	0.5	0.5	1	0, 1
<i>Camponotus lateralis</i>	65	42	0	0	0	0.5	0
<i>Colobopsis truncata</i>	57	84	0	0	0	0	0
<i>Lasius lasioides</i>	49	11	1	0	0	0	0, 1
<i>Camponotus cruentatus</i>	41	0	1	0	0	0.5	0, 1
<i>Cataglyphis spp.</i> <sup>a</sup>	24	0	0	0	0	0	1
<i>Temnothorax racovitzai</i>	16	0	0	0	0	0.5	0, 1
<i>Tapinoma cf. nigerrimum</i>	11	5	1	1	1	1	0
<i>Iberoformica subrufa</i>	5	0	0	0	0	0.5	0, 1
<i>Tetramorium forte</i>	5	0	1	0	0	1	1, 0.5
<i>Cardiocondyla batesii</i>	3	0	0	0	0	0.5	0, 1
<i>Plagiolepis schmitzii</i>	3	0	0	1	0.5	0.5	0
<i>Camponotus fallax</i>	0	37	0	0	0	0.5	0
<i>Lasius grandis</i>	0	21	1	0	0	1	0, 1
<i>Formica cunicularia</i>	0	5	0	0	0.5	0.5	0, 1
<i>Tapinoma erraticum</i>	0	5	1	1	1	1	0

Species are sorted by their percentage occurrence (%) in the sampled trees in 1992 (N = 37 trees). Ant species in 2016 and their percentage of occurrence is also showed (N = 19 trees). Four life history traits related to competition in ant communities are given, following Arnan et al. (2012, 2017). Behavioral dominance (Dom): dominant (1) and subordinate (0). Number of queens (Queen): polygyny (1), monogyny (0) or both (0.5). Number of nests (Nest): polydomy (1), monodomy (0) or both (0.5). Foraging strategy (Forage): mass recruitment (1), group recruitment (0.5), individual foraging (0). Diet: liquid food (0), seeds (0.5) or insects (1). The Argentine ant is added as a comparison for these traits

<sup>a</sup>*Cataglyphis spp.* corresponds to two species, *C. floricola* and *C. tartessica*, the latter was described in 2014 and formerly was considered the orange form of *C. floricola* (Amor and Ortega 2014)

resistance offered by dominant species could be effective under certain environmental conditions, spread across abiotic obstacles could be favored by accidental facilitation, such as, human-driven jumps. For example, it has been shown that, at the global scale, long-distance Argentine ant dispersal is typically mediated by unintentional human transport (Suarez et al. 2001). Humans can also enable more local, short-distance jumps (Carpintero et al. 2005; Angulo et al. 2011), which are otherwise unlikely because of the wingless queens.

In this study, we aim to assess the relative roles of different factors affecting the spread of the Argentine ant at a local scale in a Mediterranean ecosystem with favorable habitats (cork oak trees) interspersed within an unfavorable scrubland matrix. We used a temporal approach, comparing snapshot-annual data of ant communities collected through three different decades

(in 1992, 2000 and 2016) during the spread of the Argentine ant in the area. First, we tested whether the native species richness or the proportion of dominant ants in uninvaded cork oak trees in 1992 could be limiting the future invasion by Argentine ants. We hypothesized that trees with low ant species richness or low proportion of dominant ants would be invaded first, following the biotic resistance hypothesis. In order to further explore this hypothesis, we analyzed whether the community composition was related to the process of the invasion. We hypothesized that trees that were invaded first would have a different species composition compared to the ones that were not invaded. Alternatively, we explored the possibility that spread to new trees is facilitated by other factors. In the study area, transport of *L. humile* by humans and by scavenger raptors, which may take ant-infested carrion items to their nests, has been qualitatively

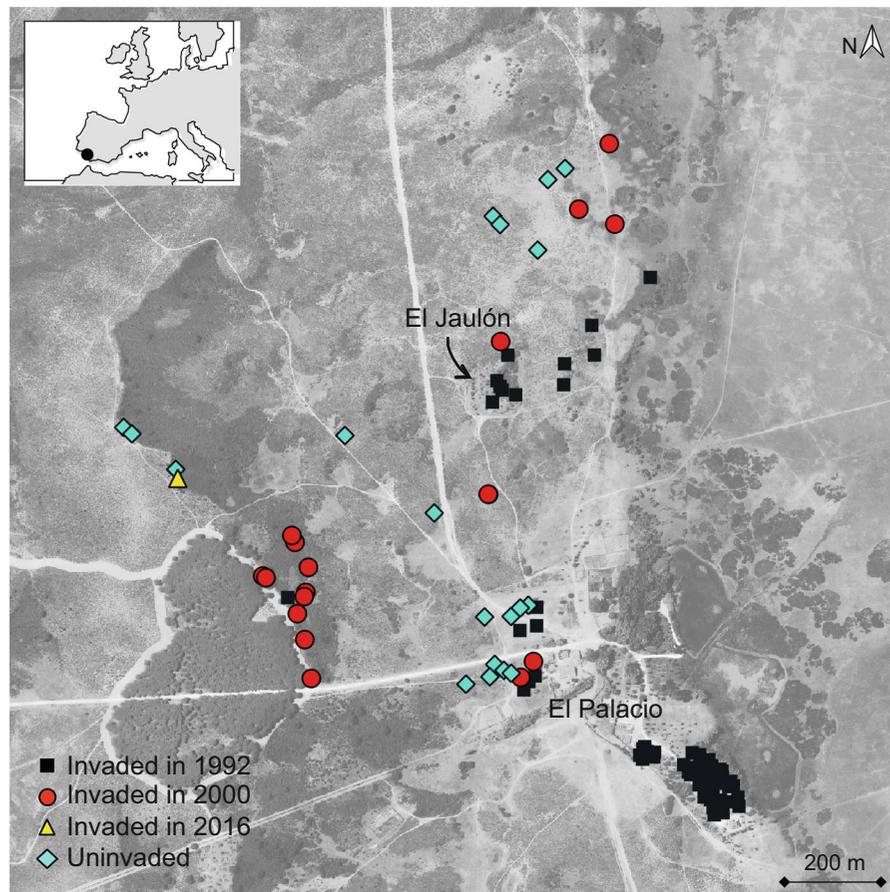
suggested to influence the invasion of new trees (Carpintero et al. 2005; Angulo et al. 2011). In these cases, we would expect that the Argentine ant spread would be linked to roads and paths, or to the breeding sites of scavenging raptors.

## Materials and methods

### Study area

Sampling was conducted in Doñana Biological Reserve of Doñana National Park (37°1'N, 6°33'W), situated on the Southwest coast of Spain, in an open Mediterranean scrubland containing scattered pine forests (*Pinus pinea*) and isolated cork oak trees

(*Quercus suber*) (Fig. 1). The study area is inhabited by more than 30 ant species, and the Argentine ant is the only invasive species (Carpintero et al. 2004). The first invasion focal point was the building of El Palacio de Doñana, the Reserve's field-research station with year-round human presence of some 3–50 people, where the Argentine ant was first detected in 1970 (Angulo et al. 2011). Due to its low tolerance of high temperatures and dry habitats, its range in natural habitats is mainly restricted to individual cork oaks or pine forests (Angulo et al. 2011). The first time the Argentine ant was seen in a natural area of Doñana National Park was in the 1980's in a cork oak in El Jaulón (Carpintero et al. 2005), a human construction that very likely constituted a second invasion focal point (Fig. 1). Thus, in our study, isolated cork oak



**Fig. 1** Study area: the main focal points for the invasion of the Argentine ant, El Palacio and El Jaulón, are marked. The study area consists of a matrix of unfavorable dry Mediterranean scrubland containing scattered cork oak trees, which act as favorable habitat patches. Trees that were invaded in 1992 are

marked by black squares, trees that were invaded in 2000 are marked by red circles, and trees that were still not invaded in 2000 are marked by light blue diamonds. The only tree invaded between 2000 and 2016 is marked by a yellow triangle

trees constitute our sampling units in order to follow the invasion progress of the Argentine ant.

### Sampling the ant community

In June 2016 we repeated, using the same protocol, the sampling that Carpintero et al. (2005) performed in 1992 and 2000. They sampled the ant community at all the cork oaks within 1.5 km of the invasion focal point, El Palacio. At each tree, during 10 min, we looked for the different ant species, native or invasive, patrolling trunk and branches from 0.5 to 2 m high. We considered a tree invaded if the Argentine ant was present on it. In general, when the Argentine ant successfully invades a tree, it replaces all other native ant species, so its detection is very likely (Angulo et al. 2011). Samples of native ant species were collected and kept in 70% alcohol for subsequent identification by the authors in the laboratory.

From the 182 trees Carpintero et al. (2005) sampled, we excluded the ones that were not alive in 2016, and three trees that had two trunks one beside the other were considered only one tree. Thus, we get an initial sample size of 105 trees in 1992, of which only 38 were uninvaded at that time. Of these 38 trees, 18 had been invaded by 2000 and only a single additional tree had been invaded by 2016 (Fig. 1). Therefore, because expansion virtually halted after 2000 in the sampled area, here we focus on the process of invasion that occurred between 1992–2000, which covers a significant invasion expansion. Trees were categorized by their invasion status as “uninvaded” if they remained uninvaded in 2000 ( $N = 19$ ) or “invaded” if they were invaded in 2000 ( $N = 18$ ; Fig. 1), with a total number of 37 cork oaks.

### Ant community structure

A matrix of presence-absence of each native ant species found in the 1992 survey was constructed for the 37 trees selected for the analysis. We compared the native ant community between trees that were subsequently invaded in 2000 or remained uninvaded by this year (invasion status). We performed a permutational multivariate analysis of variance (PERMANOVA) using the *adonis* function (package *Vegan*, Oksanen et al. 2016) in R (R Studio version 1.0.136, RStudio Team 2016).

To graphically represent differences in community structure by invasion status, we performed a non-metric multidimensional scaling test (NMDS), using the *metaMDS* function with 1000 iterations (package *Vegan*, Oksanen et al. 2016) in R (RStudio Team 2016). This analysis represents the original position of each community in multidimensional space. We chose the appropriate number of dimensions by examining the stress value (correct below 0.1). Trees were differentiated by their invasion status using the *ggplot* function (package *ggplot2*, Wickham 2009), which draws 95% confidence interval ellipses.

We were interested in whether the ant community of uninvaded trees had changed. We performed a second PERMANOVA and NMDS (as described before) to compare ant communities in 1992 and in 2016, using only trees that remained uninvaded in 2016 ( $N = 19$ ).

### Anthropogenic, biotic and abiotic variables affecting the invasion of new trees

In order to know which parameters affected the invasion of new trees since 1992, we performed a generalized lineal model using the *glm* function (package *stats*, R Core Team 2015). The dependent variable was the status of invasion (invaded or uninvaded in 2000) and we modeled it with a quasibinomial link distribution. We estimated the following parameters that we fitted to the model as independent variables:

- (a) Ant species richness: number of native ant species for each cork oak tree in 1992. Species richness was added to the model in order to test the biotic resistance hypothesis, under the prediction that less species-rich trees would be liable to invasion.
- (b) Behavioral dominance of native species: we separated the native species found in 1992 in each cork oak tree by their position in the behavioral dominance hierarchy, classing each as dominant or subordinate, following Arnan et al. (2012, 2017) (Table 1). We estimated the percentage of dominant species from the total number of native species present. Our prediction was that a lower proportion of dominant species would increase the likelihood of invasion.

- (c) **Spatial variables:** The geographic coordinates (latitude and longitude) of each tree were added to the model to take into account the spatial arrangement of trees. We used a geographic information system (QGIS, version 2.18.14, QGIS 2013) to calculate distances from each sampled tree to three potential invasion sources: El Palacio, El Jaulón, and the nearest invaded cork oak, with the tool “measure line”. We only used the minimum of these distances, to take into account the proximity of each tree to the closest potential invasion source.
- (d) **Surrounding habitat quality:** Argentine ant expansion is limited by dryness and high temperatures of the scrubland matrix around cork oak trees (Angulo et al. 2011). The normalized difference vegetation index (NDVI) measures, through satellite imagery, visible and near infrared light reflected by plants, and is an estimate of the density and quality of the vegetation of a certain area (Karkauskaite et al. 2017). NDVI was measured in a circle of 100 m of radius around the trunk of the tree by accessing Landsat images of  $30 \times 30$  pixels, using the function *create buffer* in QGIS 2.18.14 (QGIS 2013). For each tree we calculated yearly measures as the average of monthly measures (0–3 measures per month were available) and then used the average of the yearly measures from 1992 to 2000. Higher NDVI means more productivity and more vegetation cover, implying lower aridity and thus a better habitat quality for the Argentine ant. We also measured the perimeter of each trunk (cm) at 1.5 m height, because bigger trees provide more vegetation cover, humidity and lower temperatures than smaller trees (Angulo et al. 2011).
- (e) **Dispersal by humans:** we calculated the minimum distance from each sampled tree to the nearest path. Because humans may inadvertently transport ant queens in their cars or with their belongings, lower distances to paths would mean higher probability of ant queen transport to cork oaks. We used the same tool as in (c) to calculate the minimum distance.
- (f) **Dispersal by raptors:** Black and Red kites (*Milvus migrans* and *M. milvus*, respectively) breed in large numbers in the study area, mainly using cork oaks and pine trees as support for

their nest (Sergio et al. 2005). Both species are wide-ranging facultative scavengers, very adept at finding animal carcasses, even very small ones, such as meat items from human refuse (e.g., Kumar et al. 2018). During the breeding season, prey items are usually transported to the nest or to feeding perches, typically located within 10–50 m from the nest. We used historical data from kite surveys conducted between 1992 and 2000 (details in Sergio et al. 2005) to obtain: (1) the total number of kite nests situated in a 50 m radius centered on the trunk of each cork oak, and (2) the total number of nestlings that were raised in those nests each year. Because both variables were correlated ( $R^2 = 0.88$ ,  $p < 0.001$ ,  $N = 37$ ), we chose to include in the model only the number of nests. We assumed that more nests would lead to higher probabilities of accidentally transporting queen ants that were feeding on the carrion item when this was picked up and taken to the nest area by a kite, thus dispersing the ants.

Statistical differences for each of the above independent variables were obtained with the function *drop1* and the F statistic (package *stats*, R Core Team 2015). We used a backward stepwise procedure in order to obtain a final model that only included statistically significant variables (Table 2).

## Results

Of the total 105 cork oaks that survived the three decades of study, 67 were already invaded in 1992, 18 were invaded from 1992 to 2000 and just one more had been invaded by 2016 (Fig. 1). We also observed trees that were invaded but were found devoid of Argentine ants in subsequent years. This occurred in eight trees: six were invaded in 1992, of which three had native ants in 2000 and the other three had native ants in 2016; two trees that were invaded in 2000 had native ants in 2016.

### Differences in ant community structure between invaded and uninvaded trees

The community analysis did not show significant differences in the native ant community

**Table 2** Effects of anthropogenic, biotic and abiotic variables in the invasion of new trees

	Complete model		Final model		
	F	<i>p</i>	F	<i>p</i>	Sign
Species richness	2.53	0.124	17.32	< 0.001	(+)
Dominant species (%)	0.54	0.741	–	–	–
Distance to an invasion source	18.43	< 0.001	56.73	< 0.001	(–)
NDVI	0.03	0.869	–	–	–
Tree perimeter	2.10	0.159	–	–	–
Distance to a path	20.52	< 0.001	34.84	< 0.001	(–)
Number of nests	3.01	0.094	6.68	0.015	(+)
Latitude	0.62	0.440	26.12	< 0.001	(+)
Longitude	1.29	0.266	39.10	< 0.001	(+)

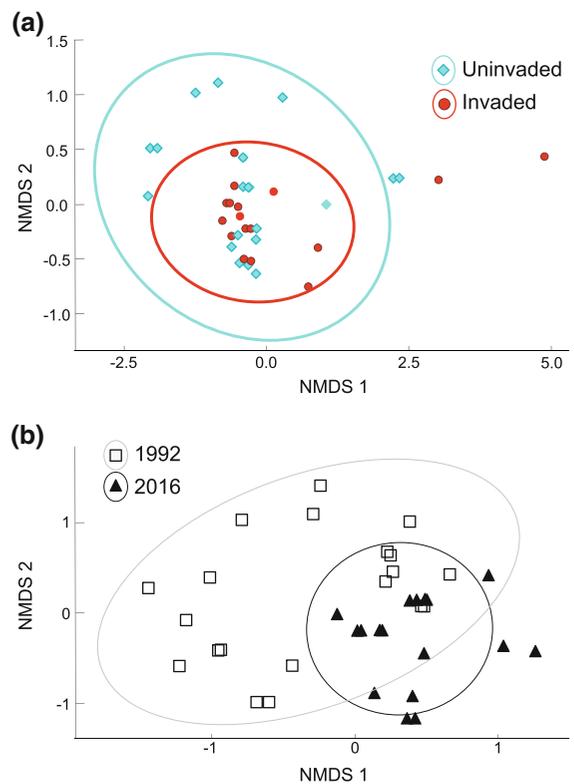
(PERMANOVA,  $F = 1.63$ ,  $p = 0.141$ ,  $N = 37$ ) between the trees that were invaded or uninvaded in 2000. We ran NMDS with two dimensions and had a fair stress value of 0.05. As shown in Fig. 2a, the ant community structure of invaded and uninvaded trees was very similar, the only difference being a wider ant community in uninvaded trees, suggesting that ant communities of the invaded trees could be a subgroup of the ant communities of uninvaded trees.

The ant community of uninvaded trees significantly changed between 1992 and 2016 (PERMANOVA,  $F = 6.23$ ,  $p = 0.001$ ,  $N = 19$ , Fig. 2b). While the ant community in 1992 contains more species than in 2016, the two communities are largely overlapping, differing in some species that have been substituted for others with similar ecological functions (Table 1).

Anthropogenic, biotic and abiotic variables affecting the invasion of new trees

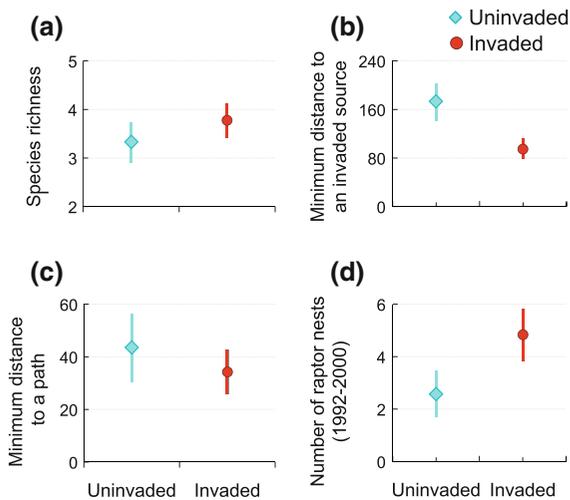
When testing the biotic resistance hypothesis, we found that species richness was selected as an important variable in the final regression model ( $F = 17.32$ ,  $p < 0.001$ ,  $N = 37$ , Fig. 3a, Table 2). However, the sign of the relationship implied no biotic resistance to invasion by the native community. Indeed, we found the opposite result: trees with higher native ant richness were more likely to be invaded. The behavioral dominance hypothesis was also not supported: the percentage of dominant species in each cork oak was not selected as a significant variable in the final model.

Geographic effects were important for the invasion process: the invasion of new trees depended on the



**Fig. 2** Ordination of ant community similarity (NMDS) for **a** trees that were invaded by Argentine ants (red circles) or that were still devoid of the invading species by 2000 (light blue diamonds); **b** ant communities in un-invaded trees in 1992 (white squares) and in 2016 (black triangles). The ellipses represent the 95% confidence interval for each group

distance to the nearest source of invasion ( $F = 56.73$ ,  $p < 0.001$ ,  $N = 37$ , Fig. 3b; Table 2). Latitude and longitude also had a significant effect, showing an invasion pattern that moved preferentially to the north



**Fig. 3** Characteristics of trees invaded (red circles) or uninvaded (light blue diamonds) by the Argentine ant. **a** Average ( $\pm$  SE) of native ant species richness in 1992; **b** average ( $\pm$  SE) of the minimum distance to an invaded source (invaded tree or invasion focal point); **c** average ( $\pm$  SE) of the minimum distance to a path; **d** average ( $\pm$  SE) of total number of nests of scavenger raptors in invaded trees or in trees that remained uninvaded by 2000. Raptor nests include those of *Milvus milvus* and *M. migrans* in a 50 m circle around the tree for the period 1992–2000

and west ( $F = 39.10$  and  $F = 26.12$  respectively;  $p < 0.001$ ,  $N = 37$  in both cases, Table 2).

In relation to the tree quality and its environment, neither the perimeter of tree trunk in 1992 nor the NDVI index were selected as important variables in the final model (Fig. ESM\_1, Table 2). Finally, anthropogenic and raptor facilitation were supported by our results: the likelihood of invasion increased with the proximity to a path ( $F = 34.84$ ,  $p < 0.001$ ,  $N = 37$ ; Fig. 3c; Table 2) and with the number of kite nests in the immediate surroundings ( $F = 6.68$ ,  $p = 0.015$ ,  $N = 37$ , Fig. 3d; Table 2).

## Discussion

We followed the invasion of *L. humile* at a local scale during three different decades (1992, 2000 and 2016), studying different biotic and abiotic factors that can influence the process, in a protected area with favorable habitats interspersed with unfavorable ones. We found that the invasion moved from main focal invasion points towards the closest trees and that the likelihood of invasion increased with the proximity to

a path. The native ant community did not offer resistance to the invasion, neither in terms of species richness, nor in proportion of dominant species or community structure. However, our results suggest that raptors facilitate ant dispersal towards areas that would not be accessible to the Argentine ant by itself.

Most of the literature dealing with biotic resistance against the Argentine ant shows that native ants are not able to resist the invasion when abiotic conditions are adequate for the invader. Exceptions found in the bibliography include communities that contain dominant native species, such as *T. nigerrimum* in Corsica, which can limit the spread and establishment of this invader (Blight et al. 2010). Although *T. cf. nigerrimum* was found in 11% of the cork oak trees we studied, its presence did not seem to prevent invasion. *T. simrothi*, another dominant species that is ecologically similar to *T. cf. nigerrimum*, was shown by Way et al. (1997) to be displaced by the Argentine ant as well. Dominant species also have a role in the first steps of invasion: a higher propagule size (e.g., a larger Argentine ant colony size) is needed for successful invasion in the presence of dominant species such as *I. rufoniger* in Australia (Walters and Mackay 2005), *Pheidole megacephala* in South Africa (Mothapo and Wossler 2014) or *Monomorium antarcticum* in New Zealand (Sagata and Lester 2009).

Given the local juxtaposition of habitat conditions, the invasion of new trees in our study area could be accomplished by diffusion (e.g., “budding”, where a group of workers and queens colonize new areas on foot) or by leapfrog advances, depending on whether trees are separated by favorable or unfavorable habitat (Suarez et al. 2001). Such jumps would consist of a small propagule size, and thus the effects of dominant species could have a role in preventing such new invasions. Among the five dominant species in our study area, the one that was more frequent in the trees before invasion was the native arboreal ant *C. scutellaris* (located in more than 75% of the trees). This species is aggressive and territorial, but does not always display polygyny and polydomy (two characteristics that if present could make their arboreal nests less vulnerable to Argentine ants); that may be the reason why it was systematically displaced during the invasion (Way et al. 1997; Angulo et al. 2011). When abiotic conditions are unfavorable for the invasion, native species can coexist and compete with Argentine ants for resources, thus slowing down the invasion

(Menke et al. 2007). Examples include *Solenopsis molesta*, *Leptothorax andrei* and *Prenolepis imparis* in Southern California (Suarez et al. 1998).

Despite the above, neither the proportion of dominant species nor species richness prevented the spread of the invader in our system. Studies in other Mediterranean climates such as the chaparral of Southern California (Menke et al. 2007) and the coastal scrub of Australia (Rowles and O'Dowd 2007) have also shown a lack of biotic resistance by native ants when abiotic conditions were favorable for the invasion. However, biotic resistance has been reported to be more effective in natural than in urban habitats (Helford 2012). Although Doñana is a natural area, the invasion is for the moment concentrated in the surroundings of a small, permanent human settlement, which could help the Argentine ant to persist against natives.

The analysis of ant community structure suggested that trees that resisted the invasion had a wider community structure than the trees that were invaded. This does not mean that they were simply composed of more species, but rather that they were organized differently, suggesting the possibility that the key to biotic resistance against invasion may not be the number of species or percentage of dominants, but rather a certain combination of species. Moreover, natural ant communities change over time, especially in isolated trees (Gove et al. 2009; Donoso 2017). In our case, ant communities of uninvaded trees differed between 1992 and 2016. The changes did not seem a result of Argentine ant invasion, but rather consisted of substitution between ecologically similar native ant species. More research should be done in order to assess this effect.

However, contrary to the biotic resistance hypothesis, our results showed that cork oaks with higher ant species richness were invaded first. Holway (1998) found that, although invasion rate was independent of native ant richness, it increased with native ant abundance. In fact, larger trees are the ones that have resources capable of maintaining more species (Kurz-Benson et al. 2006). Although in our analyses the perimeter of the tree was not a significant variable for the invasion, we also observed that larger trees had more ant species (see Fig. ESM\_2a). Larger trees also support higher abundances of aphids (Ward et al. 1998), which may facilitate invasion because aphid honeydew is one of the main food sources for the

Argentine ant (Shik and Silverman 2013). Both the native ant *C. scutellaris*, and the invasive Argentine ant use honeydew resources in cork oaks (Abril et al. 2007). And in our study area, ant abundance in trails on the tree trunk was correlated with the size of the tree (see Fig. ESM\_2b), suggesting that bigger trees sustain bigger colonies, probably because of the greatest availability of resources, such as aphids. In addition, larger tree crowns provide more shade, which is likely to result in temperatures conducive to Argentine ant survival. Holway (2005) and Angulo et al. (2011) found that Argentine ants were more abundant in habitats with more vegetation cover and moisture, while in the scrubland they were less abundant and more likely to coexist with native species (Way et al. 1997; Holway 2005; Menke et al. 2007; Rowles and O'Dowd 2007; Roura-Pascual et al. 2011).

The presence of unfavorable dry scrubland areas separating the favorable habitat constituted by the cork oak trees has very likely slowed the expansion of the Argentine ant during these past decades. According to the review of Suarez et al. (2001), the maximum annual rate of spread of the Argentine ant invasion is  $154 \pm 21$  m (range 15–275 m), which means that in Doñana it could have spread as far as 3.7 km (range 360–6.6 km) between 1992 and 2016. However, since 1992 only 19 of the 37 uninvaded trees in the study area were colonized, and since 2000 only one new tree was colonized, while 18 trees remain uninvaded. This occurred within a sampling area of 1.5 km radius from the main invasion focal point, where the maximum distance from the main invasion focal point to an invaded tree was 509 m in 1992. Thus, the local Argentine ant population does not seem capable of saturating its already colonized range. Moreover, we detected eight invaded trees that were subsequently devoid of Argentine ants and which were colonized again by native ants (six of these trees were already invaded in 1992 and two were invaded in 2000). This is not a rare situation. Menke et al. (2018) also found evidence of invasion retreat in Northern California, probably caused by the severe drought that the State had suffered during four consecutive years. Cooling et al. (2012) found a population collapse of the Argentine ant in New Zealand that allowed the native populations to recover, perhaps due to abiotic conditions like high rainfall or to inbreeding depression.

Although trees that were closer to the invasion source were invaded earlier, the Argentine ant has reached areas that are surrounded by unfavorable and uninvaded habitats. It is widely known that humans are dispersal vectors of the Argentine ant (Suarez et al. 2001; Ward et al. 2005; Boser et al. 2017), and proximity to paths frequently used by humans was previously suggested as a factor contributing to spread across unfavorable areas in Doñana National Park (Carpintero et al. 2005). Our results add quantitative support to this idea, showing that trees that were closer to a path were invaded earlier.

Moreover, Carpintero et al. (2005) proposed that, among vertebrates, scavenging raptors could facilitate the invasion of new trees across unfavorable habitat, and our results lend quantitative support to this hypothesis. The invasion of a tree was related to the abundance of kite nests in the surrounding habitat. Because the Argentine ant is a scavenger species (Angulo et al. 2011), it is possible to find it feeding on animal carcasses or meat refuse from humans. Queens are also sometimes present on such food items (authors' pers. obs.). When ant-infested food items are picked up and transported by kites to their nest areas, there is a chance that the propagule could be transported to an area inaccessible to the Argentine ants alone. This scenario could explain the leapfrog invasion of some isolated trees in the north of our sampling area (see Fig. 1). Although this mode of spread may be of relatively minor importance compared with the large-scale, sometimes inter-continental, human-mediated jump dispersal, it could be of importance in natural areas where large avian predators are common, where human presence is less pervasive, or where management actions have been attempted to reduce human-mediated ant dispersal. For example, at our study site, measures to prevent the inadvertent transport of Argentine ant propagules by humans have been established since 2004. These measures include substituting concrete for wood in fencing, directives for secure transport of food, garbage and other human materials from houses to the rest of the protected area, and adequate transport and conservation of organic materials used in experiments or for scientific collections. Additional routes of human-related dispersal should be taken in account when studying invasion patterns: soil movements (used for path restoration and other infrastructures), translocations of plant specimens grown in invaded

areas, or constructions of underground infrastructures (which ants could use as refugia or dispersion routes to new areas). Transport by raptors cannot be prevented, especially by wide-ranging raptors such as kites that may forage in rubbish dumps tens of kilometers outside of the protected area (Heredia et al. 1991).

Independently of the local situation, the possibility that mobile vertebrate predators, such as avian facultative scavengers, can act as vectors of invasive species is relatively new in invasion ecology and adds a new dimension to invasion management and prevention. Note that some avian facultative scavengers are opportunistic-adaptable species that can be locally common in both urban and natural areas. For example, black kites are extremely abundant within urban environments of Africa and southern Asia, where they subsist almost entirely on human subsidies and refuse, reaching the highest raptor densities ever recorded (Kumar et al. 2018). Their potential as vectors of ant dispersal in these environments, or their synergy with human dispersal, would be even greater than portrayed here. In conclusion, our study lends support to previous ones suggesting that biotic resistance *per se* is unlikely to halt Argentine ant invasion, even in environments with an overall unfavourable matrix. Furthermore, colonization maintenance and spread may be supported not only by humans but also by mobile predators, whose dispersal capabilities should be considered when planning the management of invasive species.

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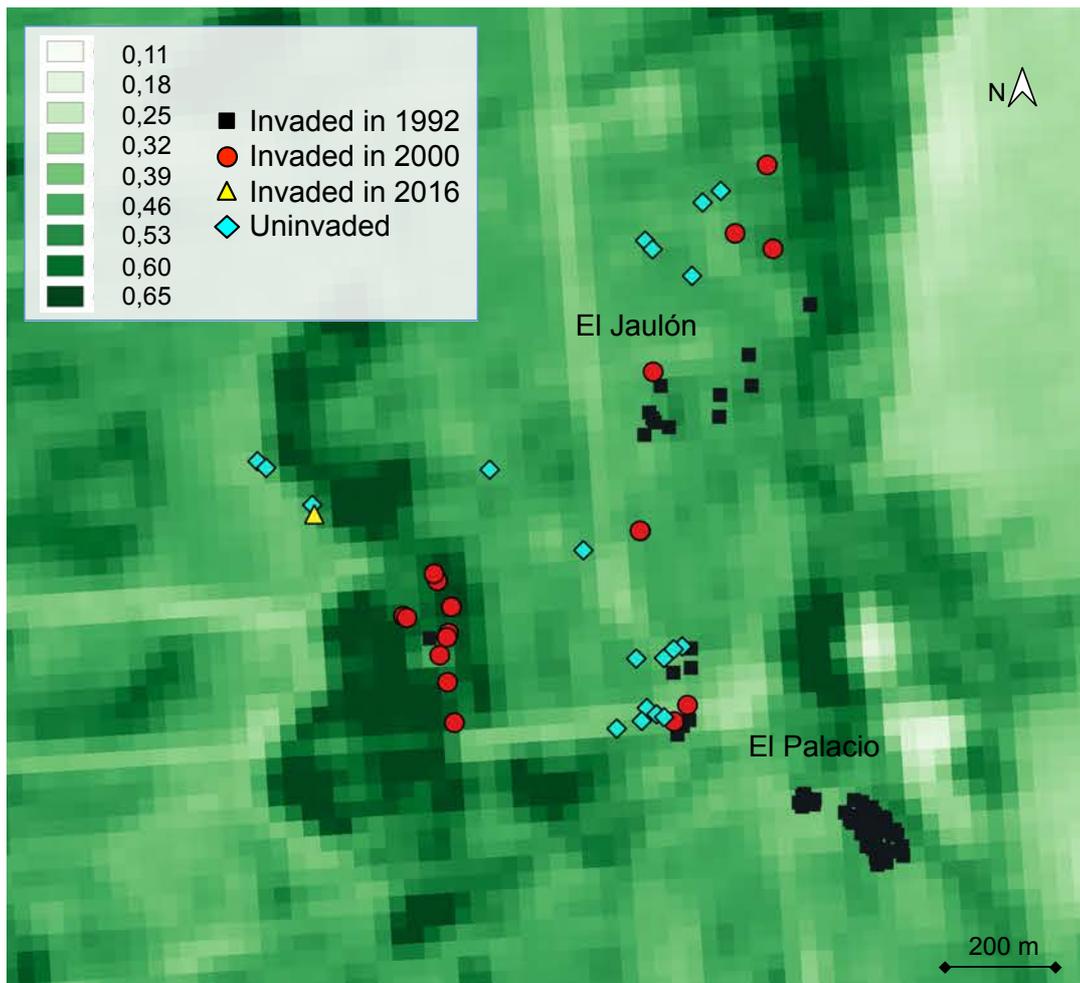
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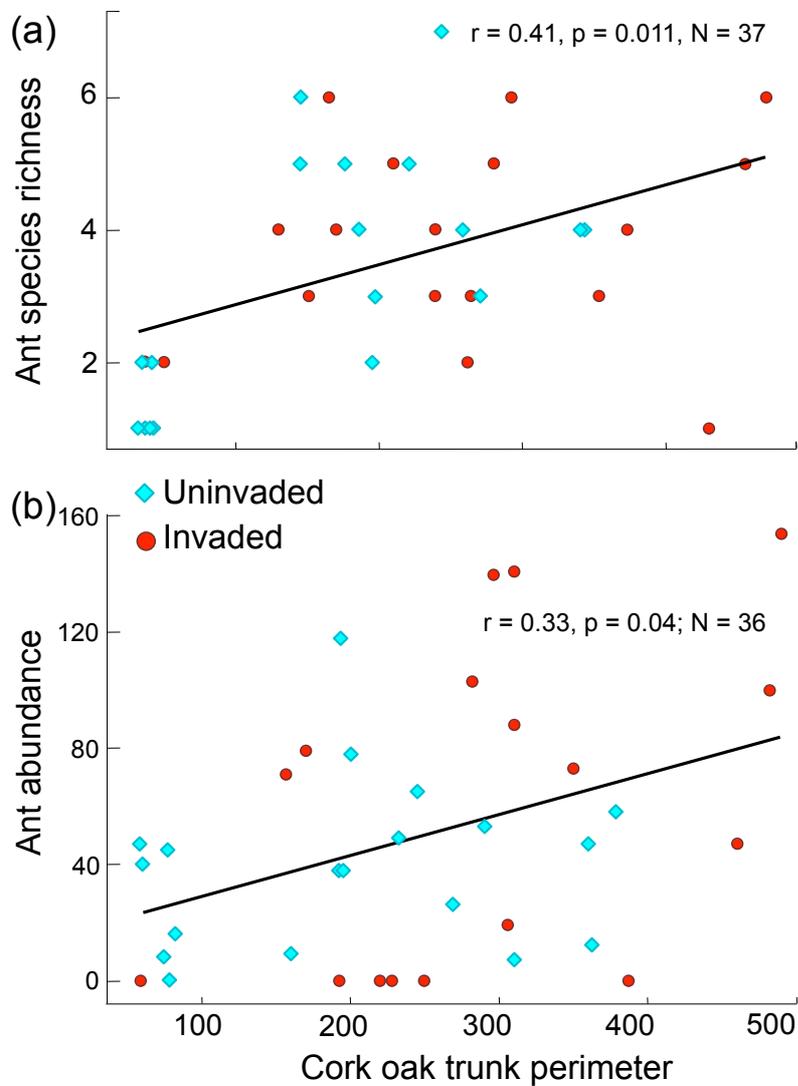
**Humans and scavenging raptors facilitate Argentine ant invasion in Doñana National Park: no counter-effect of biotic resistance**

Sara Castro-Cobo · Soledad Carpintero · Joaquín L. Reyes-López · Fabrizio Sergio · Elena Angulo

**Figure ESM\_1.** Mean NDVI values (1992-2000) in the study area. Data is provided for 30x30 pixels. Higher values represent higher density and quality of the vegetation (see Methods). In our case higher values corresponded to trees, mainly cork oak trees, pine trees, and poplars, and to the wet scrubland, which is constituted mainly by *Erica* spp., *Ulex* spp. and *Rubus ulmifolius*. The lowest values corresponded to paths, marshlands and ponds. Intermediate values corresponded to the dry scrubland constituted mainly by *Halimium* spp., *Ulex* spp., *Cistus* spp., *Lavandula stoechas* and *Thymus mastichina*.



**Figure ESM\_2.** Relationships between the size of the cork oak tree with ant species richness (a) and ant abundance (b). In (a) trunk perimeter and ant richness correspond to the year 1992 when all these trees were uninvaded (but they have been distinguished by their invasion status in 2000). In (b) trunk perimeter and ant abundance correspond to the year 2016 (we do not have ant abundance for the previous years). Ant abundance was estimated as the number of ants per minute, counted in the thickest vertical ant trail of each tree. Data comes from invaded (red circles) and uninvaded (light blue diamonds) trees; in (b) data corresponds to the abundance of Argentine ants and native ants, respectively. Native ants measured were *Crematogaster scutellaris* and *Lasius grandis* (N = 16 and N=2 respectively). We show the fit and statistics for the correlation tests performed, which were done with the cor.test function, , in the 'stats' package of R (Core Team 2015).



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