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Effects of wildfires on behavioral dominance dynamics in Spanish ant communities

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Author contributions

Study conception and design were performed by Raphaël Boulay and Xim Cerdá. Material preparation and data collection were performed by José Manuel Vidal-Cordero and Eirini Linardaki. Analysis was performed by José Manuel Vidal-Cordero and Elena Angulo. The first draft of the manuscript was written by José Manuel Vidal-Cordero, and Elena Angulo and Xim Cerdá commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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41 **Abstract**

42 Fire can have a variety of effects on ant community structure and composition, resulting from
43 indirect changes in habitat structure, microclimate, resource availability, and competitive
44 interactions. However, there is no research examining how ant behavior may differ following a
45 fire. We analyzed how fire affects behavioral dominance dynamics at three similar sites in
46 southwestern Spain that had burned in different years (2012, 2014, and 2016) sampled in 1017.
47 We characterized the outcome of competitive interactions between ant species on different bait
48 types in two burned plots and two unburned plots at each study site. We had four main results.
49 First, the mean number of interactions was similar for burned and unburned plots and was not
50 influenced by time since fire. Second, the higher temperatures in the burned plots favored the
51 competitive success of ecologically subordinate species at baits. Third, bait discovery was
52 influenced by time since fire, was significantly faster in the burned plots where the baits were
53 always discovered by ecologically subordinate thermophilic species; in the unburned plots,
54 ecologically dominant species were the first to find the baits. Fourth, we did not observe an
55 inverse relationship between species behavioral dominance at baits and bait discovery ability;
56 but most species had a discovery-defense strategy: they could discover baits rapidly and then
57 defend those baits against other species. We hypothesize that the absence of true behaviorally
58 dominant species – which were actually behaviorally subdominant – allows this discovery-
59 defense strategy to operate successfully, meaning that ecologically subordinate species were
60 not excluded from food resources.

61 **Significant statement:** Wildfires strongly affect plant and animal communities. Ant communities
62 are hierarchical, consisting of dominant and subordinate species that share resources at
63 different times of the day based on thermal preferences. Here, we studied how fire alters
64 competitive interactions among ant species at baits by comparing burned and unburned sites,
65 and how these behaviors recover over time since a fire. The number of competitive interactions

stayed the same after fires, but burned areas became warmer, favoring the success of heat-tolerant, ecologically subordinate species. These subordinate species were the first to discover baits in burned areas, whereas dominant ants discovered them first in unburned areas. Additionally, subordinate species discovered baits faster, especially in recently burned areas. Finally, most species displayed a discovery-defense strategy: because strictly dominant ants were absent, subordinate ants were not excluded, allowing them to successfully access food resources post-fire.

Keywords: behavioral dominance, competition, discovery time, ecological dominance, hierarchies.

Introduction

Natural disturbances such as hurricanes, earthquakes, floods, droughts, and forest fires have been shaping ecosystems and species ecology for millennia. The resulting effects on ecosystem structure and function are widely recognized (Mart-Jan et al. 2003; Coyle et al. 2017). Forest fires are the most frequent type of disturbance (Sommerfeld et al. 2018). They are also the most commonly studied disturbance (Viljur et al. 2022) because they affect conservation efforts worldwide, making it essential to understand the impacts of fires on biodiversity (Mart-Jan et al. 2003; Coyle et al. 2017; Kelly et al. 2020; Viljur et al. 2022).

Wildfires have highly variable ecological effects because they have diverse drivers and because initial system properties differ dramatically (Peters et al. 2023). In the immediate term, wildfires directly destroy vegetation, fauna, and the soil microbiome (Scott et al. 2014; Köster et al. 2021). In the longer term, wildfires have indirect effects because of the ways in which they change ecosystems. These changes can negatively affect plant composition and recovery (Tyler 1995; Laughlin and Fulé 2008); soil physiochemical conditions and, consequently, microbial mortality (Köster et al. 2021); and soil carbon loss and soil organic carbon decomposition

(Mekonnen et al. 2022). Furthermore, wildfires frequently modify resource availability or abiotic conditions, create landscape heterogeneity, increase biodiversity, and renew or reorganize ecosystems (Seidl et al. 2017; Seidl and Turner 2022).

To date, research on the ecological impacts of fire has largely focused on plants (Keeley et al. 2011, 2012). However, over the last decade, there has been an increase in studies focused on animals in general (Engstrom 2010; Beale et al. 2018; Nimmo et al. 2018, 2021; Pausas and Parr 2018; Pausas 2019; Jolly et al. 2022) and insects in particular (New 2014). Research on ants has tended to examine how fire affects taxonomic richness and abundance (Farji-Brener et al. 2002; Parr et al. 2004; Moretti et al. 2004; Arnan et al. 2006; Sackmann and Farji-Brener 2006; Kwon 2015; Anjos et al. 2015, 2017; Vasconcelos et al. 2017; Adams et al. 2018; Rosa et al. 2021; Bonoan and McCarthy 2022; Staff et al. 2023); in some cases, the effects on functional diversity have also been explored (Arnan et al. 2013, 2020; Bishop et al. 2021; Vidal-Cordero et al. 2022, 2023). Another research focus has been the longer-term effects of fire on specific ecological responses such as ant-mediated seed dispersal (Arnan et al. 2009; Beaumont et al. 2013, 2018), colony production of females (Caut et al. 2014), diet shifts (Lázaro-González et al. 2013), and cavity use by arboreal ants (Arruda et al. 2020). Finally, recent studies have shown that fire can affect ant behavior, specifically interspecific patterns of dominance (Sensenig et al. 2017; Tavella and Cagnolo 2018).

Fire mainly affects ant communities indirectly, via its impacts on habitat structure, microclimate, resource availability, and competitive interactions (Andersen et al. 2019). The result may be changes in ant richness, abundance, or composition (Arnan et al. 2006; Anjos et al. 2017; Vidal-Cordero et al. 2022, 2023), as well as in patterns of species co-occurrence (Tavella and Cagnolo 2018). Tavella and Cagnolo (2018) found that, after a fire, there were shifts in interaction composition and species roles, even though species richness and aggregated network properties remained unchanged; they also found that the changes in species roles

115 translated into turnover in pairwise species interactions in a way that was shaped by site fire
116 regime. Sensenig et al. (2017) observed that, in Kenya, fire can increase ant colony mortality and
117 decrease ant colony size, disrupting mutualistic associations between acacia trees and dominant
118 ant species. These dynamics favor subordinate ant species, which are more fire resilient, and
119 thus maintain diversity despite the existence of an established dominance hierarchy (Sensenig
120 et al. 2017). In conclusion, it is essential to study the effects of fire on ant functional ecology,
121 such as dominance dynamics, if we wish to better understand how fire impacts ant communities.

122 Dominance is a frequently misused term, and it is important to clearly define what it
123 means in relation to interspecific competition among ants occupying the same guild (Cerdá et
124 al. 2013). According to Cerdá et al. (1997), there are two types of species dominance in ant
125 communities: 1) behavioral dominance, where dominant species consistently competitively
126 exclude subordinate species at food resources when species interact directly and 2) ecological
127 dominance, where dominant species occupy food resources in higher proportion than expected
128 according to their abundance. Recently, Stuble et al. (2017) explored the limitations of the
129 dominance hierarchies commonly used in research on ant communities, highlighting that they
130 are essentially just ranking species based on behavioral dominance (i.e., greater likelihood of
131 winning interspecific encounters) or numerical dominance (i.e., greater relative abundance).

132 In the Mediterranean, research has focused on how fire affects the ecological responses
133 of certain ant species (Lázaro-González et al. 2013; Caut et al. 2014) or ant taxonomic and
134 functional diversity (Arnan et al. 2013, 2020; Vidal-Cordero et al. 2022, 2023). However, nothing
135 is known about the influence of fire on behavioral dominance dynamics in ant communities. In
136 this study, we analyzed the effects of fire on ant dominance dynamics in three areas of
137 southwestern Spain that had experienced fires in different years. We expected that fire and time
138 since fire would influence the roles and identities of the species in ant communities and that
139 these changes would be associated with shifts in behavioral dominance. We had four specific

hypotheses. First, we expected the number of interactions at resources to be greater in more recently burned plots than in less recently burned plots, given that species richness has been found to increase after fires due to the appearance of subordinate and opportunistic species. Second, we predicted that, in more recently burned plots, the absence of vegetation would lead to higher ground temperatures for longer periods during the day and that these higher temperatures would favor the competitive success of subordinate species in interactions at resources; in contrast, we predicted that, in less recently burned plots, the presence of vegetation would lead to more shade and lower temperatures, favoring the competitive success of dominant species in interactions at resources. Third, we expected that, in more recently burned plots, the reduced habitat complexity would facilitate foraging activity in general, resulting in faster resource discovery and longer resource occupation by more subordinate and thermophilic species; we expected to see the opposite pattern in less recently burned plots, characterized by greater habitat complexity. Fourth, we predicted that, if a trade-off between resource discovery and dominance were to occur, it would be more evident in less recently burned plots, where more dominant species are expected to be more abundant.

Materials and methods

Study sites

The study was conducted in the Huelva province in Andalusia (southwestern Spain; Fig. 1a,b). Our three study sites were near Moguer (37°12'N, 6°44'W, 55 m above sea level), El Campillo (37°44'N, 6°41'W, 241 m above sea level), and Gibraleón (37°14'N, 7°1'W, 10 m above sea level), respectively. The ecosystem was the same at the three sites: pine forest dominated by *Pinus pinea* with an understory generally composed of *Cistus ladanifer*, *Ulex* sp., *Pistacia lentiscus*, *Halimium halimifolium*, *Cistus monspeliensis*, and *Chamaerops humilis*. Each site had experienced a crown fire that had wiped out all the vegetation; the fire had occurred in 2016 at

Gibraleón (1 year before the study), 2014 at El Campillo (3 years before the study), and 2012 at Moguer (5 years before the study).

At each study site, we established four sampling plots: two plots in an unburned area of the site and two plots in a burned area of the site. The plots were separated by 100–300 m (Fig. 1c). To characterize the vegetation structure in the burned and unburned areas, we set up a transect (75 m long, 10 m wide) in each sampling plot. Then, every 5 m along the transect, we recorded the presence or absence of herbaceous plants, low shrubs, high shrubs, and trees, identifying plants to species (see Supplementary Materials for details about the plant cover analysis).

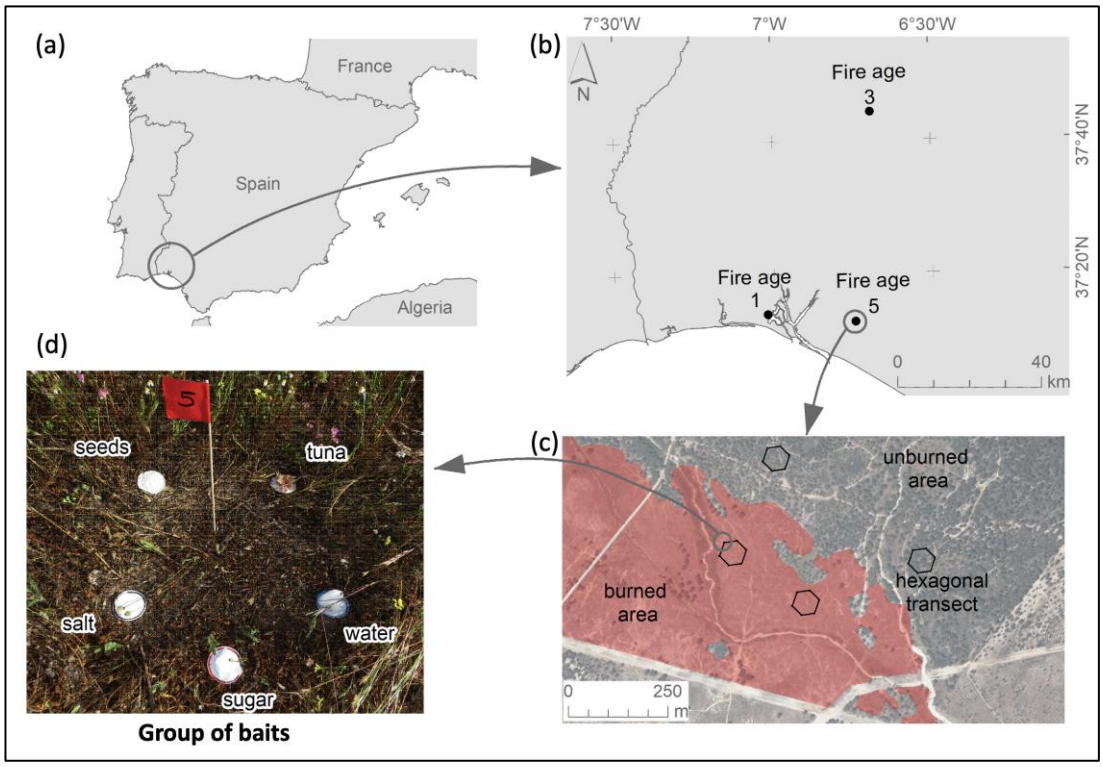


Fig. 1 *(a) Map of the general study area and (b) specific study sites (black dots), (c) the four hexagonal bait transects (plots) at an example study site and (d) the structure of a bait group. The numbers next to the study sites indicate the time since the fire in years. A group of five baits was positioned at each vertex of the hexagonal transect*

Bait trials

In 2017, we carried out bait trials during 3-5 days per plot in May (spring sampling period) and June–July (summer sampling period). At each study site, bait trials were performed at three times of day: in the morning (9:00–11:30), at midday (12:30–15:00), and in the afternoon (18:00–20:30). In each sampling plot, we set up a transect in the form of a hexagon, with a bait group at each of the six vertices (Fig. 1c). The bait groups were 10 m apart. Each bait group contained five bait types: sugar (20% concentration in water), salt (NaCl; 1% concentration in water), water, tuna, and sesame seeds. The baits were placed on plastic circles (bases of plastic cups with the cup walls cut away; diameter: 50 mm), which were arranged in a pentagon (Fig. 1d). Two bait types were placed directly on the plastic circles: the tuna (crumbs of canned tuna packed in water) and the sesame seeds (hulled). For the three liquid baits (sugar, salt, and water), cotton balls soaked in each liquid were placed on the plastic circles. The tuna was considered to be a high-protein bait (25–29% protein), and the sesame seeds were considered to be a high-fat bait (50–58% fat, 17–18% protein).

During each trial, each bait group was visited 5, 15, 30, 60, 90, and 120 min after bait placement. During each visit, we recorded the time, the ground surface temperature at the center of the bait group (infrared thermometer: PCE instruments PCE-777N; measurement taken at a height of 1 m), and the abundance of each ant species associated with each bait type in the group. When ants could not be identified to species in the field, we sampled individuals, storing them in ethanol until identification could take place in the laboratory. It was not possible to record data blind because our study involved focal animals in the field. We then measured discovery time for each bait group: it was the time at which we observed the first arrival of an ant at any of the group's five baits. If none of a group's baits were discovered, the discovery time was the maximum observation time, which was 120 min.

Competitive interactions and behavioral dominance

We constructed competition hierarchies based on the outcomes of the direct interactions between the ant species that we observed at the baits: we considered that a species was competitively successful when it drove a competitor away, and we considered that a species was competitively unsuccessful when it was driven away by a competitor. We calculated a behavioral dominance index (DI) value for each species based on all the paired interactions between species that we observed at the baits:

DI value = % success = [(N cases where species was successful) / (N cases overall (species was successful + species was unsuccessful)] * 100,

DI values were obtained for each species for each study plot (burned and unburned) at each study site, and the competition hierarchies were built using the results.

Behavioral interactions and dominance

First, we determined whether the number of interactions was influenced by fire status (burned or unburned) and time since fire (1, 3, or 5 years) using a generalized linear model (GLMM; *glmer.nb* function in *lme4* package, Bates et al. 2015) with a negative binomial distribution (Poisson distribution was tested but resulted in overdispersion, See R scripts in Supplementary Material). The dependent variable was the number of interactions per plot (sum of interactions across the five bait types and six bait groups) at each sampling time point (5, 15, 30, 60, 90, 120 min). Fire status, time since fire, and their interaction were included as fixed independent variables; additional independent variables were time of day (morning, midday, or afternoon) and sampling period (spring or summer). Bait group number (1 to 24) was included as a random variable to account for the repeated measures over time in the plots.

Second, we determined whether the competitive outcomes at the baits (success or failure) were influenced by fire status (burned or unburned) and time since fire (1, 3, or 5 years). We carried out two sets of analyses: one for ecologically dominant ants and one for ecologically subordinate ants, using the categories in Arnan et al. 2014. The goal was to clarify whether the same factors affected competitive success for the ecologically dominant versus ecologically subordinate ants. We used generalized linear models (GLMs; *glm* function in *stats* package, R Core Team, 2024) with a binomial distribution, as the dependent variable was competitive success or failure in the interaction. The fixed independent variables were fire status (unburned or burned), time since fire (1, 3, or 5 years), their interaction, and ground surface temperature. Additional independent variables were time of day (morning, midday, or afternoon) and sampling period (spring or summer).

Third, we characterized the behavioral dominance hierarchy for the species in each ant community. We created matrices in which species were ranked by their DI values (dominance index), where a higher DI value corresponded to a higher level of behavioral dominance. Matrices were created for each fire status (burned and unburned areas) and time since fire (1, 3, and 5 years).

Bait discovery, bait dominance, and the dominance-discovery trade-off

First, we calculated the percentage of baits occupied by each species for the different categories of fire status (burned and unburned), time since fire (1, 3, and 5 years), and time of day (morning, midday, and afternoon) (Fig. S1).

Second, we explored whether discovery time was influenced by fire status (burned or unburned), time since fire (1, 3, and 5 years), or their interaction. We carried out a linear mixed model (LMM; *lmer* function in *lme4* package, Bates et al. 2015) in which the dependent variable was discovery time. The fixed independent variables were fire status (burned or unburned), time

since fire (1, 3, and 5 years), their interaction, and ground surface temperature. Additional independent variables were time of day (morning, midday, or afternoon) and sampling period (spring or summer). Group bait number (1 to 24) was included as a random variable. Then, we carried out independent models for each time of day.

Third, we calculated the mean discovery time of the bait groups. We also determined the number of baits occupied at the first sampling time point (5 min) for each ant species, which we used as a proxy for species discovery ability. We ranked the species accordingly—the top-ranked discoverer was the species that occupied the largest number of baits at 5 min.

Finally, to determine whether there was evidence for a trade-off between bait dominance and bait discovery (described by Fellers 1987), we used the number of baits occupied at the last sampling time point (120 min) as a proxy of species dominance ability and ranked the species accordingly. We then explored whether there was an association between the species dominance ranks and discovery ranks.

Results

Behavioral interactions

The mean number of interactions per plot was influenced by time since fire and the interaction between fire status and time since fire ($X^2 = 31.66$, $p < 0.001$, $X^2 = 20.86$, $p < 0.001$, respectively; $N = 432$); there was no influence of fire status by itself ($X^2 = 0.04$, $p = 0.363$) (Fig. 2). Additional independent variables were also significant ($X^2 = 16.93$, $p = 0.002$ and $X^2 = 6.95$, $p = 0.008$, for time of day and sampling period respectively).

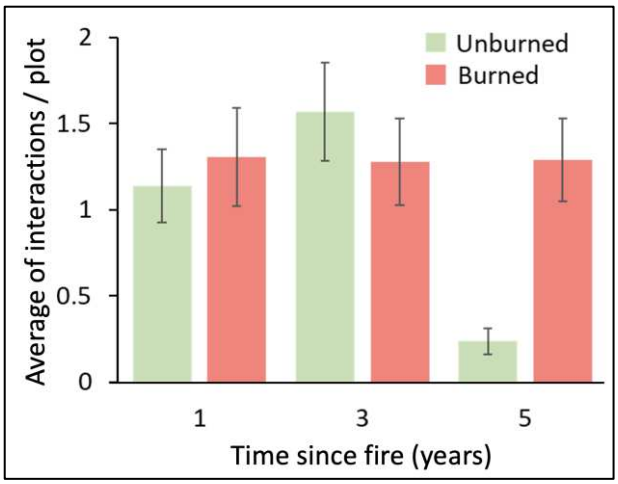


Fig. 2 *Number of interactions (mean ± SE) in burned and unburned plots at the three study sites, which differed in time since fire (1, 3, and 5 years)*

264

265 For ecologically dominant species, the variables affecting competitive success at baits
266 were ground surface temperature (X^2 = 6.31, p = 0.011), time since fire (X^2 = 7.11, p = 0.028), fire
267 status (X^2 = 7.97, p = 0.005), and the interaction between fire status and time since fire (X^2 =
268 12.10, p = 0.002) (N = 415, Fig. 3). Time of day and sampling period were not significant (X^2 =
269 2.73, p = 0.255, X^2 = 3.03, p = 0.082, respectively). In contrast, for ecologically subordinate
270 species, only ground surface temperature and fire status affected competitive success at baits
271 (X^2 = 9.29, p = 0.002; X^2 = 4.89, p = 0.027, respectively N = 567). None of the other variables
272 affected their competitive success at baits (time since fire: X^2 = 4.33, p = 0.115; status x time
273 interaction: X^2 = 4.86, p = 0.088; time of day: X^2 = 0.79, p = 0.671; sampling period: X^2 = 3.29, p
274 = 0.070).

275 At all the study sites, most competitive interactions in both the unburned and burned
276 plots occurred at ground surface temperatures of 25–38°C (Fig. 3). However, in the burned plots,
277 most of the competitive interactions involving ecologically subordinate species occurred at
278 ground surface temperatures of 30–49°C.

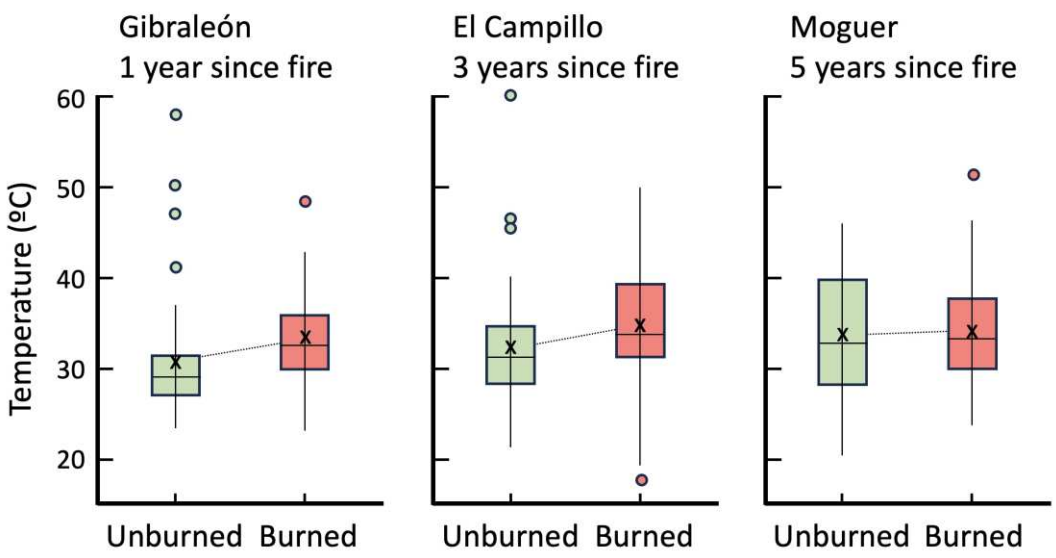


Fig. 3 *Influence of temperature on interaction success for dominant ant species at the three study sites, which differed in time since fire (1, 3, and 5 years)*

279

280 The DI values allowed us to explore how time since fire influenced behavioral dominance
281 in the ant communities (Fig. 4). At Gibraleón (1 year since fire), greater differences were seen
282 between the burned and unburned plots than at El Campillo (3 years since fire) or Moguer (5
283 years since fire). Specifically, at Gibraleón, more species appeared and disappeared, and species
284 frequently changed positions within the behavioral dominance hierarchy (up to 5 positions, Fig.
285 4a). There were fewer such shifts (0–2 positions) at El Campillo (3 years since fire) and Moguer
286 (5 years since fire, Fig. 4b,c). Overall, in the unburned plots, the first four positions of the
287 hierarchy (DI values > 1.5) were occupied by ecologically dominant ants in the genus
288 *Crematogaster* as well as ecologically subordinate ants in the genus *Plagiolepis*; other top-
289 ranked species included *Pheidole pallidula* (Gibraleón—1 year since fire), *Iberoformica subrufa*
290 (El Campillo—3 years since fire), *Tetramorium* species (El Campillo and Moguer—3 and 5 years
291 since fire), and *Aphaenogaster* species (Moguer—5 years since fire) (Fig. 4).

292 Overall, in the burned plots, the ecologically dominant *Crematogaster auberti* was in the
293 top position, and *Tetramorium* species were in the second or third positions (DI values > 2).
294 Other top-ranked species in the burned plots were *Tapinoma nigerrimum* (second position at

295 Gibraleón—1 year since fire), *I. subrufa* (second position at El Campillo—3 years since fire) and

296 *P. pallidula* and *Tetramorium forte* (second position at Moguer—5 years since fire) (Fig. 4).

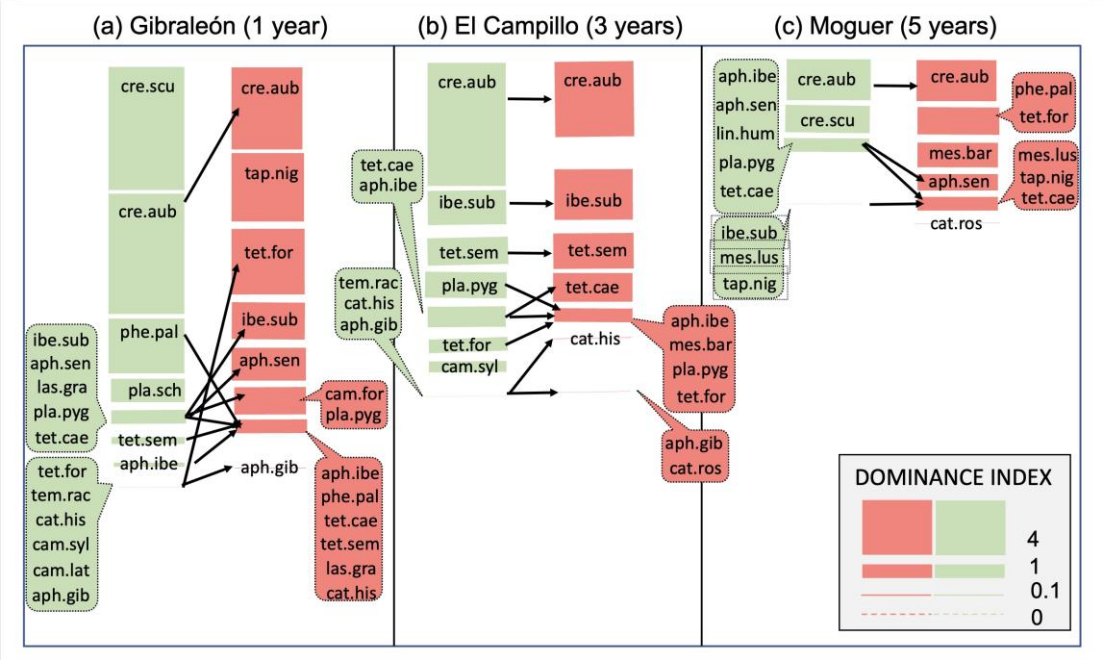


Fig. 4 *Changes in the behavioral dominance hierarchy of the ant community in the unburned plots (green) and burned plots (red) at each study site: (a) Gibraleón (1 year since fire); (b) El Campillo (3 years since fire); (c) Moguer (5 years since fire). Dominance was determined based on the outcomes of interspecific interactions at baits, which were used to calculate the dominance index (DI) values. Box thickness reflects the DI values. Species abbreviations are indicated in Table S2*

297 *Discovery time*

298 Overall, mean bait discovery time was influenced by fire status ($F = 15.88$, $p < 0.001$), time since

299 fire ($F = 6.92$, $p = 0.001$), and their interaction ($F = 7.42$, $p < 0.001$) as well as by sampling period

300 ($F = 19.92$, $p < 0.0001$) and ground surface temperature ($F = 29.29$, $p < 0.0001$) ($N = 432$; Fig. 5a).

301 The same pattern was seen during the morning bait trials (fire status: $F = 15.46$, $p < 0.001$; time

302 since fire: $F = 3.22$, $p = 0.043$; status x time interaction: $F = 6.82$, $p = 0.001$; ground surface

303 temperature: $F = 11.32$, $p = 0.001$) ($N = 432$; Fig. 5b). At midday, there was still an influence of

304 fire status ($F = 10.92$, $p = 0.002$), time since fire ($F = 12.43$, $p < 0.0001$), and ground surface

temperature ($F = 30.19$, $p < 0.0001$) but not of the interaction between fire status and time since fire ($F = 0.80$, $p = 0.457$) ($N = 432$; Fig. 5c). In the afternoon, discovery time was only influenced by ground surface temperature ($F = 5.25$, $p = 0.023$) but not by fire status ($F = 0.54$, $p = 0.462$), time since fire ($F = 2.44$, $p = 0.091$), or their interaction ($F = 0.93$, $p = 0.398$) ($N = 432$; Fig. 5d).

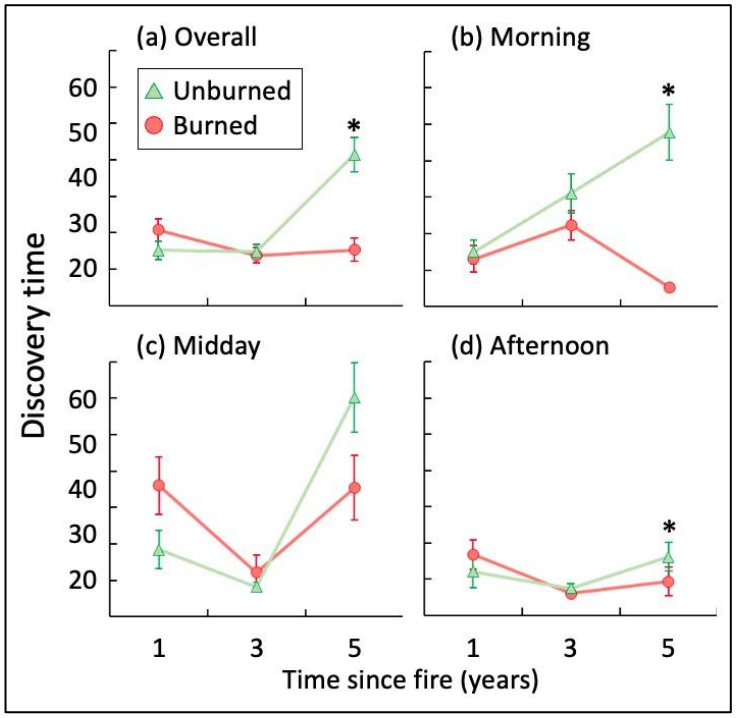


Fig. 5 *Discovery time (mean ± SE) for the three study sites with different times since fire: (a) overall; (b) in the morning; (c) at midday; and (d) in the afternoon*

We observed that the identity of the top-ranked discoverers in the unburned plots differed across the three study sites (Fig. 6): the ecologically dominant species *Crematogaster scutellaris* was the best discoverer at Gibraleón (1 year since fire, Fig. 6a), while this position was held by the ecologically subordinate species *Cataglyphis hispanica* at El Campillo (3 years since fire, Fig. 6b) and the ecologically dominant *Tapinoma nigerrimum* at Moguer (5 years since fire, Fig. 6c). In the burned plots of Gibraleón (1 year since fire) and Moguer (5 years since fire), *Aphaenogaster senilis* was the top discoverer (Fig. 6d,f); in the burned plots of El Campillo (3 years since fire), the species in this position was the same as in the unburned plots: *C. hispanica* (Fig. 6e).

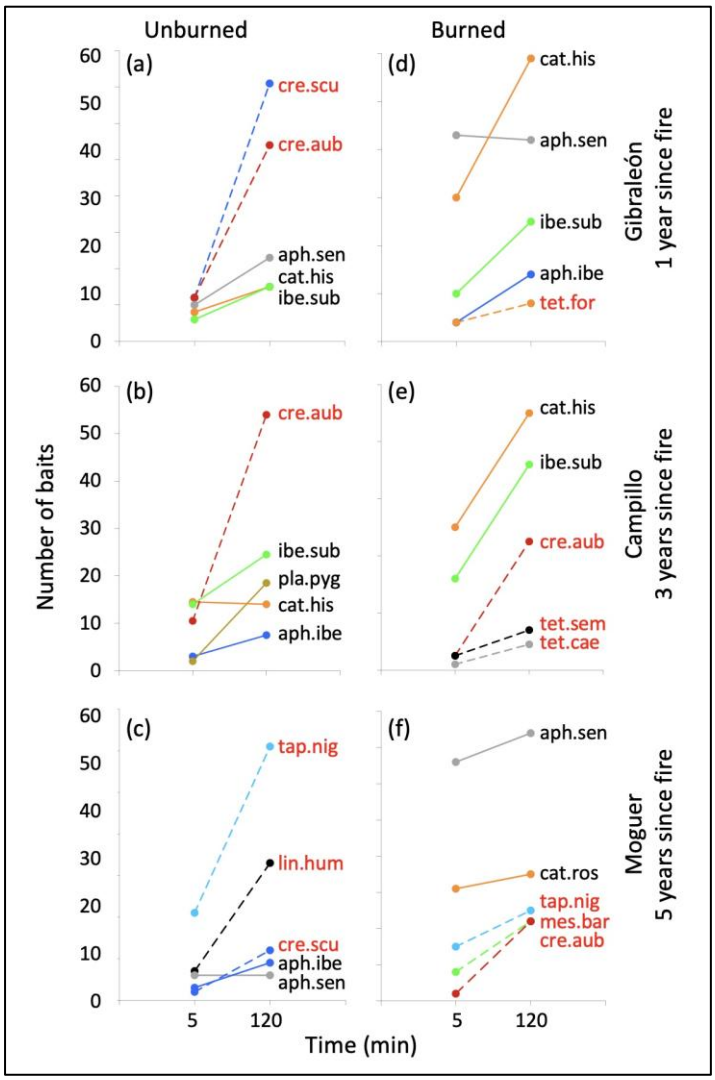


Fig. 6 *Changes in bait occupation between the first sampling time point of 5 min and the last sampling time point of 120 min focusing on the five top discoverers in the burned and unburned plots at the three study sites. Species abbreviations are indicated in Table S2 (ecologically dominant species are in red with dashed lines)*

319

320 *Bait occupation*

321 We used bait occupation at 120 min to rank species dominance ability. The top-ranked species
322 in the unburned plots were *C. scutellaris* at Gibraleón (1 year since fire, Fig. 7a), *C. auberti* at El
323 Campillo (3 years since fire, Fig. 7b), and *T. nigerrimum* at Moguer (5 years since fire, Fig. 7c),

while the top-ranked species in the burned plots of all three study sites were ecologically subordinate species: *Cataglyphis* species, *A. senilis*, and *I. subrufa* (Fig. 7). In the unburned plots, the top-ranked species were consistent across all three times of day (with the exception of *T. nigerrimum*, which disappeared at midday). In contrast, in the burned plots, the rankings often shifted. At midday, *Cataglyphis* species occupied the greatest percentage of baits, while in the morning and afternoon, other ecologically subordinate species (e.g., *A. senilis*, *I. subrufa*) occupied the greatest percentage of baits (Fig. S1 and S2).

Bait dominance and dominance-discovery trade-off

We did not observe an inverse species-level relationship between the dominance ranks (bait occupation at 120 min) and the discovery ranks (bait occupation at 5 min). In most cases, the species that discovered a given bait then dominated that bait for the entire observation period (Fig. 6). This pattern was seen in both the burned and unburned plots. The most striking result was that ecologically subordinate species had high dominance ranks when dominance was determined using bait occupation at 120 min. Such was seen not only in the burned plots, but also in the unburned plots of El Campillo (3 years since fire), where *C. hispanica* maintained a relatively high dominance rank.

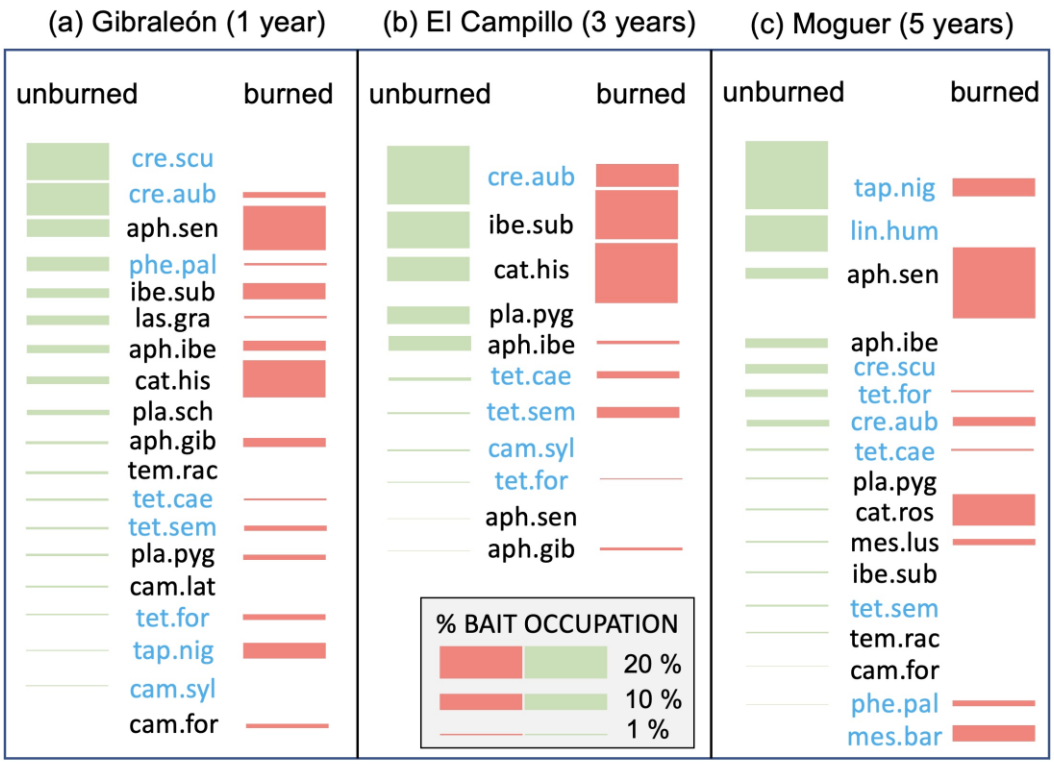


Fig. 7 *Percent bait occupation by ant species in unburned and burned plots at the three study sites: (a) Gibraleón (1 year since fire; N = 1,113 observations in unburned plots, 1,101 observations in burned plots); (b) El Campillo (3 years since fire; N = 1,182 observations in unburned plots, 1,130 observations in burned plots); (c) Moguer (5 years since fire; N = 643 observations in unburned plots, 1,051 observations in burned plots). Box thickness reflects percent bait occupation. Species abbreviations are indicated in Table S2; the species in blue are behaviorally dominant*

Discussion

Our study is the first to examine how fire can elicit behavioral differences in ant communities. It may be that this topic was left unexplored because it is difficult to detect behavioral changes. Our first hypothesis was that the number of interactions at baits should be greater in more recently burned plots because species richness has been found to increase after fires due to the appearance of subordinate and opportunistic species. Previous research has shown that fire can change species roles and the nature of species interactions without changing species richness and interaction network macrostructure (Tavella and Cagnolo 2018). Interestingly, we found

348 that the mean number of interactions was similar in both burned and unburned plots and that
349 there was no influence of time since fire. However, it is important to note that the number of
350 interactions per transect was extremely low (lower than 2). By comparison, Cerdá et al. (1997)
351 observed approximately 20 to 100 interspecific interactions at baits in other Mediterranean ant
352 communities, and similar numbers of interactions have been seen in the relatively species-poor
353 ant communities of Doñana National Park (Sánchez-García et al. 2022). One possible explanation
354 to be explored in the future is that both habitat types in this study (unburned pine forest and
355 open burned areas) have very low levels of ant abundance, resulting in a rarity of interspecific
356 encounters. Another reason why fire did not appear to influence the number of interactions in
357 our study could be that the ant species that disappeared after the fires were replaced by
358 opportunistic and newly arrived species, leading to a similar frequency of interactions. If such is
359 the case, the concept of functional redundancy (Houadria et al. 2016) may apply, where the
360 influence of species richness depends on the relative functional contribution of the most
361 efficient species.

362 Our second hypothesis was that the absence of vegetation in the more recently burned
363 plots would result in higher ground surface temperatures, favoring the success of ecologically
364 subordinate heat-tolerant species in direct competitive interactions at baits (Cerdá et al. 1997);
365 in contrast, we predicted that less recently burned plots would have more developed
366 vegetation, with more shade and lower ground surface temperatures, favoring the success of
367 ecologically dominant heat-intolerant species in direct competitive interactions at baits. Our
368 results show that most interactions occurred within a temperature range of 25–38°C, the range
369 within which the ants carry out their daily activities (Cros et al. 1997). However, as we expected,
370 the higher ground surface temperatures in the burned plots favored the success of the
371 ecologically subordinate species. The latter participated in interactions (both successfully and
372 unsuccessfully) under a wider range of temperatures (29–49°C) than did the ecologically

dominant species. In addition, in the burned plots, this temperature range was greater with greater time since fire because less recently burned plots had herbaceous plants and low shrubs, resulting in more of a temperature mosaic.

We also found that higher ground surface temperatures positively affected the competitive success of both ecologically dominant and ecologically subordinate species during interactions at baits. However, time since fire only had an influence on the success of the ecologically dominant species, not on the success of the ecologically subordinate species. This result contrasts with what was seen by Cerdá et al. (1997), where higher temperatures allowed subordinate heat-tolerant species to outcompete dominant species in interactions at baits. Our finding is probably due to the species composition of the burned and unburned plots, where some of the ecologically subordinate species are opportunist and heat-tolerant (e.g., *Cataglyphis* species, *I. subrufa*, *Aphaenogaster* species) and can forage at high temperatures (Cerdá et al. 1998a; Cerdá et al. 2009), while the ecologically dominant species in the unburned plots (e.g., *C. scutellaris* or *L. grandis*) are heat-intolerant and have narrower thermal niches (Cerdá et al. 1998a, 1998b).

Because the ecologically subordinate species did not appear to benefit from a thermal advantage during interactions at baits, the species with the top DI values were always the ecologically dominant species (*C. auberti* or *C. scutellaris*), regardless of fire status or time since fire. The same was true for the species with the second-highest DI values, with the exception of *I. subrufa*, which had the second highest DI value in both the burned and unburned plots at El Campillo (3 years since fire). The high rank of *I. subrufa* was likely due to its competitive success when interacting with other ecologically subordinate species, such as those in the genera *Aphaenogaster* and *Cataglyphis*. *Iberoformica subrufa* did not have a high DI value at Moguer (5 years since fire), likely because of the longer time since fire: the greater degree of forest recovery and higher levels of vegetation cover likely made the habitat less favorable to this species. While

398 *Crematogaster* species (*C. scutellaris* and *C. auberti)* had the top DI values at all three study sites,
399 *C. scutellaris* was only present in the unburned plots because it nests in trees or vegetation
400 (Vidal-Cordero et al. 2022). In contrast, *C. auberti* is a soil-dwelling ant that can nest anywhere,
401 regardless of vegetation cover.

402 Our third hypothesis was that the reduced habitat complexity in more recently burned
403 plots would facilitate ant foraging overall, accelerating the discovery of food resources. As
404 predicted, bait discovery time was significantly faster in burned plots and significantly different
405 according to time since fire. However, discovery time was influenced by time since fire in an
406 unexpected way: discovery time was fastest at El Campillo (3 years since fire), not at Gibraleón
407 (1 year since fire). Time of day also had a significant influence on discovery time: in the morning
408 and at midday, discovery time was significantly faster in the burned plots than in the unburned
409 plots. These times of day are when efficient thermophilic species are out foraging (Cerdá et al.
410 1998a), and they prefer open habitats, such as burned areas. In the afternoon, temperatures
411 are cooler, and the thermal differences between burned and unburned areas are likely less
412 pronounced; at this time of day, thermophilic species are not active.

413 We also hypothesized that, in more recently burned plots, ecologically subordinate
414 species and more thermophilic species would be the top discoverers and would spend more
415 time on the food resources that they found. Our results supported this prediction: the best
416 discoverers in the burned plots were always ecologically subordinate thermophilic species, while
417 the best discoverers in the unburned plots were ecologically dominant species.

418 Finally, we explored the possible existence of a discovery-dominance trade-off (Fellers
419 1987) using bait occupation at 5 min as a proxy for discovery ability and bait occupation at 120
420 min as a proxy for dominance ability. We did not observe a negative relationship between
421 species discovery ability and dominance ability. Instead, there was a positive relationship: most
422 of the time, the first species to discover a bait continued to dominate that bait for the full

observation period. This pattern held for both the burned and unburned plots. Other studies have also failed to find support for a dominance-discovery trade-off in ant communities in Mediterranean (Santini et al. 2007) or temperate climates (Lessard et al. 2009). One issue could be that we lack data about the abundance (prevalence) of each species. Ant ecologist Edward G. LeBrun has made the following argument: if foraging success is driven entirely by chance, highly prevalent species will discover and dominate a large fraction of the resource base, while the reverse will be true for low prevalence species; consequently, the null expectation is that the relationship between dominance and discovery ability will be positive, if traits are measured in a manner that does not account for prevalence (personal communication in Cerdá et al. 2013). We cannot ignore that these dynamics might have played a role in our study. However, if we consider species abundance data sampled at an earlier point in time (see Table S2), it is clear that the most abundant species were not the top-ranked discoverers and top-ranked dominants.

In their research on arboreal ants, Camarota et al. (2018) did not find support for a dominance-discovery trade-off. Instead, they observed a discovery-defense strategy: most species can arrive first at newly available food resources within the complex tree canopy and are then able to defend the food resources they have discovered. In our study system, we similarly observed a discovery-defense strategy, but the latter could result from the absence of true dominant species. Behaviorally dominant species exert a strong influence on other species during interspecific encounters, either because they initiate attacks or because their presence is enough to provoke avoidance behavior (Cerdá et al. 2013). Aggressively dominant species use interference competition to behaviorally exclude other ants from resources (Savolainen & Vepsäläinen 1988, Pisarski & Vepsäläinen 1989). However, at our Mediterranean study sites, ecologically dominant species (as defined in Arnan et al. 2012) are behaviorally subdominant, meaning that they win most of their competitive interactions with other species but that they are not "extirpators" (i.e., *Formica* species, *Atta* species, or *Oecophylla* species). They are relatively “peaceful” (as per Tanner and Adler, 2009) Mediterranean subdominant species that

allow subordinate species to exploit food resources. As prior research has underscored, there appears to be enough niche space for both dominant and subordinate strategies, and the niche of individual foraging occupied by subordinate species is far from being “suboptimal” (van Oudenhove et al. 2018).

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Supplementary materials

Supplementary Material S1. Vegetation cover analysis.

Table S1. Relative frequency of each vegetation cover type (A) and the results of the statistical models examining the influence of fire status and time since fire on vegetation cover (B).

Table S2. List of ant species in alphabetical order. Indicated is species-specific occurrence (number of pitfall traps in which each species occurred) and worker abundance (in parentheses, total number of individuals) in the unburned and burned plots at each study site. The species abbreviations are used in Figs. 4, 6, 7, and S2.

Figure S1. Total number of occupied baits in burned plots (gray bars) and unburned plots (white bars) at the different sampling time points (from 5 to 120 min) during the bait trials conducted at three times of day: morning (9:00–11:30), at midday (12:30–15:00), and in the afternoon (18:00–20:30). Data are shown for the most commonly occurring ant species.

Figure S2. Percent occupation of the different bait types (salt, seeds, sugar, tuna, water) by the most commonly occurring ant species in the burned (B) plots and the unburned (UB) plots. The values at the top of the bars indicate the total number of occupied baits in each case. Species abbreviations are indicated in Table S2. The first and second graphs show the results for the ecologically dominant species (as defined in Arnan et al. 2012), with the exception of *Plagiolepis pygmaea* (pla.pyg). The third graph shows the results for the ecologically subordinate species.

Supplementary Material S2. R-scripts code used for the analyses.

Supplementary Data 1. Dataset used for the analyses.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SuppMatS1.pdf
- SuppData1VidalCorderoetal.xlsx
- SuppMatS2CodeVidalCorderoetalcopia.r