

Four-year study of arthropod taxonomic and functional responses to a forest wildfire: Epigeic ants and spiders are affected differently

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ARTICLE INFO

Keywords:

Pine forest
Crown wildfire
Formicidae
Araneae
Functional diversity
Taxonomic diversity
Disturbance

ABSTRACT

When studying forest disturbances, it is essential to examine biodiversity from different perspectives, which includes considering its taxonomic and functional facets. Indeed, different taxa may respond differently based on their functional traits. We analyzed the short-term effects of a wildfire on epigeic ant and spider communities in a Mediterranean forest. We specifically hypothesized that (1) fire would initially decrease the taxonomic and functional diversity of both taxonomic communities and have a more pronounced effect on spiders than ants because spider nests are shallower than ant nests and are consequently more vulnerable to fire; (2) recovery time would be longer for spiders than ants; and (3) the responses of taxonomic and functional diversity would be dependent on the identities and functional traits of the species found in both taxa. Our results show that wildfire affected the structure and composition of both communities but had a greater influence on ants. Over the four years of the study, these effects were largely constant for ants, whereas spiders displayed recovery. The two facets of diversity showed parallel responses to fire in the structure and composition of ant communities and in the composition of spider communities. However, the taxonomic and functional structure of spider communities reacted differently. In both spiders and ants, we observed that burned plots hosted species typical of open habitats, while unburned plots hosted species typical of vegetated habitats. We highlight the importance of (1) conducting long-term post-fire monitoring to get an accurate estimate of ecosystem recovery relative to pre-fire conditions and (2) studying taxonomic and functional responses to fire in different taxa to increase the power of the ecosystem response predictions used in habitat management decisions.

1. Introduction

Natural disturbances (e.g., wind, floods, drought, and wildfires) can affect ecosystem structure and function (Mart-Jan et al., 2003; Seidl et al., 2016; Thom and Seidl 2016). Wildfire is a major disturbance, especially in boreal and Mediterranean forests (Bengtsson et al., 2000), and it can profoundly modify ecological succession, habitat structure, energy flow, and biotic community composition (Bengtsson et al., 2000; He et al., 2019; Paillet et al., 2010; Pausas et al., 2008; Pausas and Fernández-Muñoz, 2012). Furthermore, over recent decades, humans have fundamentally altered natural fire disturbance regimes, mainly via land use changes (land abandonment and forest plantations) that are exacerbated by the drier conditions resulting from climate change (Pausas and Fernández-Muñoz, 2012). Thus, understanding how plant

and animal communities respond to forest fires is crucial if we want to predict how fire could affect biodiversity in forest ecosystems and establish preliminary groundwork for management and conservation strategies.

To date, most studies exploring the effects of wildfire on forest biodiversity have focused on taxonomic diversity, as expressed via species richness and/or composition (Basset et al., 2008; Hamer and Hill, 2000). However, researchers are increasingly examining other forms of diversity, including functional diversity (Arnan et al., 2020, 2015; Hidasi-Neto et al., 2012). Changes in functional diversity can greatly influence ecosystem dynamics, stability, productivity, nutrient balance, and other functional factors (Laureto et al., 2015). Such work has generated major insights into community responses to disturbance and habitat change while concurrently clarifying the underlying

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mechanisms at play (Mouillot et al., 2013). It is often assumed that there is an asymptotic relationship between taxonomic and functional diversity, such that greater functional richness leads to greater species richness (Poos et al., 2009). However, it is important that such assumptions be verified by simultaneously applying taxonomic and functional approaches when gathering information that will ultimately inform species conservation and ecosystem management (Birkhofer et al., 2015; Lambeets et al., 2009).

Arthropods are key members of ecosystems and carry out a wide array of important functions, including nutrient cycling, decomposition, seed dispersal, plant pollination, predation, and scavenging. Although there are studies that have examined the effect of fire on arthropod diversity from a multi-taxa approach (Dawes-Gromadzki, 2007; Valkó et al., 2016), most of the research has focused on a single taxon or functional group (e.g., Langlands et al., 2011; Arnan et al., 2013; Lazárina et al., 2016). However, it is important to assess how fire affects different taxa if we wish to improve biodiversity conservation and landscape management efforts in an era of biodiversity loss. In this study, we examined two groups with contrasting ecologies: ants and spiders. With very few exceptions, Mediterranean ant species are ground-dwellers. Spiders, however, may live on the ground or in the vegetation, as is the case of orb weavers (Cardoso et al., 2011). Ant species are dietary generalists that exploit a variety of food resources, including dead insects, seeds, nectar, and honeydew (Arnan et al., 2019). Spiders, on the other hand, are predators that hunt mostly arthropod prey (Michalko and Pekár, 2016; Wise, 1995). Both ants and spiders display high levels of species diversity, are numerically dominant in most terrestrial habitats and ecosystems, provide important ecosystem services (Del Toro et al., 2012; Hogg and Daane, 2011; Michalko et al., 2019; Underwood and Quinn, 2010), and are highly sensitive to environmental change (Hsieh et al., 2003; Matevski and Schuldt, in press; Gosper et al., 2015; Tiede et al., 2017). As a result, ants and spiders have been used as indicators of ecosystem health capable of revealing the impacts of ecological disturbances (Oliver et al., 2000; Pearce and Venier, 2006; Underwood and Fisher, 2006; Céréghino et al., 2019; Tiede et al., 2017; Buchholz, 2010).

Generally, fire initially decreases the taxonomic diversity (Arnan et al., 2006; Vickers and Culin, 2014) and functional diversity (Arnan et al., 2013; Langlands et al., 2011) of both ants and spiders. However, taxonomic and functional diversity might be able to return to pre-fire levels over the course of secondary succession, according to some models (Kadmon and Benjamini, 2006). That said, there are dramatic differences in how arthropod communities respond to fire that are mediated by habitat type, fire regime, functional composition, and focal taxa (Andersen, 2019; Kral et al., 2017; New, 2014). For example, responses to fire may differ among taxa given that certain traits boost the likelihood of surviving a fire, the ability to cope with the subsequent environmental conditions, and the prospect of colonizing burned areas (Arnan et al., 2013; Bengtsson, 2002; Langlands et al., 2011). Such species traits can predict the level of community resistance (i.e., the degree of similarity in species composition immediately after a disturbance) and resilience (i.e., the time needed to recover pre-disturbance community structure and composition) in relation to fire (Moretti et al., 2006).

A fire will kill ants foraging outside their nests as well as spiders in their webs or outside their underground retreats. Consequently, in both taxa, survival is dependent on the characteristics of nesting sites, which can provide shelter during a fire event. Many ground-dwelling arthropods are able to survive canopy or low-intensity surface fires because they build their nests underground, and heat from a fire does not penetrate more than 30 cm below the ground surface (Cane and Neff, 2011; Matsuda et al., 2011). Indeed, most Mediterranean ant species nest in the soil. However, the majority of epigaeic spider species are at greater risk of exposure because their nests tend to occur under rocks, near the soil surface, or at shallow depths below the surface (Moretti et al., 2002; Underwood and Quinn, 2010). Of the species initially killed

by fire, some will be able to recolonize the newly created habitat via dispersal. Between the two taxa, spiders have much better dispersal abilities (in terms of time and distance) than do ants (Arnan et al., 2013; Bonte et al., 2003; Bonte and Saastamoinen, 2012). In addition, burned areas can be colonized by species that were not present before the fire (Arnan et al., 2006; Bonte et al., 2003). Differences in dispersal traits will determine the success of ants and spiders in colonizing or recolonizing habitats after fire.

We conducted a four-year study of the effects of a lightning-caused wildfire on the taxonomic and functional diversity of epigaeic ant and spider communities. Our study area was a Mediterranean pine forest in northeastern Spain. We tested three hypotheses. First, we expected fire to initially decrease both the taxonomic and functional diversity of ant and spider communities, with spiders showing a steeper decline than ants (i.e., ants should be more resistant than spiders). Second, we expected both the taxonomic and functional diversity of ant and spider communities to increase over time during the post-fire period, with spiders showing faster recovery than ants because spiders are among the first to arrive after fire due to their better dispersal abilities (i.e., spiders should be more resilient than ants). Lastly, we expected taxonomic and functional composition to vary between burned and unburned areas: burned areas should contain species with traits better suited to open areas (e.g., species build nests and search for food on the ground/in the soil and disperse over longer distances), while unburned areas should contain species with traits better suited to more vegetated habitats (e.g., species build nests and search for food in the vegetation and disperse over shorter distances).

2. Materials and methods

2.1. Study site

This research was conducted near the village of Salo, in northeastern Spain ($N 41^{\circ}52'$, $E 1^{\circ}38'$, 540–620 m above sea level; Appendix A Fig. A.1). This area has a typical Mediterranean climate, where mean annual temperature and rainfall are 12.4°C and 626.4 mm, respectively (Lázaro-González et al., 2013). The study site was in a rocky landscape comprising a mosaic of agricultural fields and pine forests (*Pinus nigra* and, to a lesser extent, *Pinus halepensis*). The forests had a relatively dense understory composed of common Mediterranean shrubs, including *Rosmarinus officinalis*, *Thymus vulgaris*, *Rhamnus alaternus*, and *Lavandula latifolia*. In June 2009, a crown wildfire burned through an area of 194 ha, composed by 74% of pine forests, 24% cropland, and 2% scrubland. We performed our study in a zone where almost all the pine trees had been burned away and canopy cover was limited within the burned areas and was essentially composed of the occasional surviving pine tree and resprouting holm oaks. Over all four years of the study, the density of trees and large shrubs was significantly lower in the burned area than in the unburned area. In contrast, the density of herbaceous vegetation increased significantly between 2010 and 2012 in both types of areas (Appendix B, Fig. B.1, Table B.1).

2.2. Ant and spider sampling

We established six $1,000\text{ m}^2$ ($50\text{ m} \times 20\text{ m}$) rectangular plots: four plots in the burned area (hereafter, the burned plots) and two plots in the unburned area (hereafter, the unburned plots). There were 550 m between the unburned plots; 270–1,300 m between the burned plots; and 200–2,000 m between the unburned plots and the burned plots (Appendix A Fig. A.1). Furthermore, each of the plots was located at least 100 m from the edge of the burned area. This distance is sufficient to avoid capturing epigaeic ants and spiders coming from outside the area being sampled (Rodrigo and Retana, 2006).

We used open pitfall traps without roofs to catch epigaeic ants and spiders. These traps were 20-cl plastic vials (65 mm in diameter, 95 mm deep) that were half filled with soapy water and salt. This method of

capture yields reliable assessments of both arthropod groups and has frequently been used to study ant (Parr et al., 2004; Arnan et al., 2006, 2007) and spider communities (Cardoso et al., 2008; Carvalho et al., 2012). Researchers seeking to exhaustively characterize spider communities use more than one sampling method (Cardoso et al. 2008, 2011), but we had a different aim in this study. We needed a relatively rapid assessment approach that would allow us to compare epigeic ant and spider communities between the burned and the unburned plots across time. It is for this reason that we employed pitfall trapping, a method inherently biased toward capturing epigeic, highly active species (Montgomery et al., 2021).

In each plot, 20 pitfall traps were placed along two 50-m transects; the transects were separated from each other by 15 m. Within the transects, the pitfall traps were separated by 5 m. We carried out the first round of sampling in July 2009, three weeks after the wildfire, and the second round of sampling in September 2009. Then, in 2010, 2011, and 2012, we sampled three times per year—in May, July, and September—to maximize the diversity of ants and spiders collected. Each of the 6 plots were thus sampled 11 times, and there were 66 sampling events in total: 44 in the burned plots and 22 in the unburned plots. We observed low levels of trap disturbance (54 traps disturbed/1267 traps set). We dealt with the missing data by extrapolating ant and spider occurrence and abundance data based on the total number of functional traps per plot.

During each sampling period, pitfall traps were run for a week. The biological contents of the traps were stored in 70% ethanol until identification could occur. Ants and spiders were separated out from the other invertebrates found in the traps. Ants were identified to species level. In most cases, it was only possible to identify the spiders to genus level. Juvenile spiders could not be identified with certainty beyond family level and were thus excluded from consideration in this study. The family Lynyphiidae was treated as a single taxon due to the difficulty of identifying its members to genus. In the Mediterranean, spider genus richness is considered a good proxy for species richness (Cardoso et al., 2004). To identify the ants, we used Gómez and Espadaler (2007); to resolve any doubts, we contacted Xavier Espadaler (Universitat Autònoma de Barcelona) and Joaquín Reyes (Universidad de Córdoba). To identify the spiders, we used the keys published by GIA (Barrientos, 2006); when needed, Iñigo Sánchez (ZooBotánico Jerez) helped resolve any uncertainty. In our analyses, we thus used species- and genus-level data for ants and spiders, respectively.

2.3. Life-history traits

We characterized 15 and 12 functional traits for the ant species and the spider genera, respectively. These traits represented three functional trait groups of recognized importance in ant and spider autecology and/or ecosystem functioning because they contribute to survival, persistence, and colonization. Such characteristics are highly useful for explaining how both ants (Arnan et al., 2013) and spiders (Langlands et al., 2011) respond to fire. While some spider species in the same genus have different functional traits, it is more common for congeners to share most traits. The ability to physically survive fire is associated with nesting site in ants and microhabitat use in spiders. The ability to persist after fire is associated with behavioral dominance, colony size, body size, and diet. The ability to colonize burned areas is associated with colony founding type in ants and ballooning capacity in spiders. The full description of the functional traits used in this study is provided in Appendix C (Tables C.1 and C.2). The information on ant traits came from past research (Arnan et al., 2013; Retana et al., 2015). For the spider traits, we conducted a literature search (Bell et al., 2005; Cardoso et al., 2011; Langlands et al., 2011; Pedley and Dolman, 2014; Schirmel et al., 2012). In both cases, we gathered additional trait data from unpublished sources provided by experts: Xavier Espadaler and Alberto Tinaut for ants and Jesús Miñano for spiders.

2.4. Data and statistical analyses

All the analyses were performed using R (v. 4.1.3; R Core Team 2022). To analyze the taxonomic structure and composition of ant and spider communities, we calculated species occurrence for ants and genus abundance for spiders (hereafter, ant occurrence and spider abundance). For the ants, we defined species occurrence per plot and sampling period as the number of traps in which a species occurred divided by the total number of traps in operation (i.e., relative frequency of traps in which the species occurred). We chose this definition to avoid any potential bias that could result from the pitfall traps being close to ant trails/ant nests. For the spiders, we defined genus abundance per plot and sampling period as the pooled number of individuals per trap across all the traps in operation (i.e., regardless of whether a given genus occurred in a given trap). Then, we calculated the following community indices per plot and sampling period for both groups:

(1) taxonomic richness (S) — the number of ant species or spider genera observed; (2) the Shannon diversity index (H); and (3) the taxonomic evenness index (Pielou's J).

To characterize the functional composition of ant and spider communities per plot and sampling period, we used two approaches that have been widely employed in ecological research. First, we determined the “trait average” (CWM), which conveys which traits are the most common in a community after accounting for differences in taxon presence (i.e., here, ant occurrence and spider abundance) (Laliberté and Legendre, 2010). The method for determining CWM differs depending on whether the traits are continuous or categorical. For continuous traits, CWM corresponds to the abundance-weighted mean and was calculated as follows:

$$\bar{x} = \sum_{i=1}^S p_i x_i$$

where p_i is ant occurrence or spider abundance i and x_i is the trait value for species (or genus) i . For categorical traits, CWM corresponds to the ant occurrence or spider abundance associated with each trait category.

Second, we examined “trait dissimilarity” or functional diversity (FD), which indicates the degree to which species within a community differ in their traits (Arnan et al., 2013; Ricotta and Moretti, 2011). We broke FD down into three different facets that were expressed via the following indices: functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis) (Villéger et al., 2008). Functional diversity indices can be used to help decipher the processes that structure biological communities (Mouchet et al., 2010). FRic conveys the amount of functional space filled by the community, but it does not incorporate information on relative abundances. We thus need other indices like FEve, which describes how evenly trait abundances are distributed within this functional space (Mason et al., 2005). However, FEve does not reveal patterns of species dispersion within functional trait space. Instead, this information is reflected by FDis, which estimates the mean distance in multidimensional trait space between individual species and the centroid of all species (Laliberté and Legendre 2010). These three facets thus provide a meaningful framework for quantifying this form of diversity and examining the mechanisms that underlie the links between diversity and ecosystem functions.

We employed the functcomp and dbFD functions in the FD package (v. 1.0-12; Laliberté et al., 2010) to calculate the CWM values and the FRic, FEve, and FDis values, respectively.

To analyze differences in the taxonomic and functional structure of the ant and spider communities (dependent variables: ant occurrence, spider abundance, S , H , J , FRic, FEve, and FDis), we used linear and quadratic mixed-effects models (LMMs). Quadratic models were also used because we preliminarily observed quadratic relationships between some response variables over time. To compare linear and quadratic models, we used the Akaike information criterion (AIC). We chose the model with the lowest AIC. For differences of less than two units, we retained the linear model following the principle of simplicity.

The explanatory variables were year of sampling (continuous variable), plot type (categorical variable: burned treatment vs. unburned treatment), and their interaction. Plot identity was a random effect that accounted for the same plots being repeatedly sampled over time. To meet the statistical assumptions regarding normality and homogeneity, we transformed 2 of the 14 variables used (log transformation of ant FRic and square root transformation of spider abundance). The models were carried out using the lme function in the *nlme* package (Pinheiro et al., 2020). We compared taxonomic richness, Shannon diversity, and Pielou's evenness between the burned and unburned plots for the ants and spiders using sample-based rarefaction curves that included data for the entire four years of the study. We built one curve per plot using EstimateS 9.1.0 (Colwell, 2009).

We employed permutational analysis of variance (PERMANOVA; the Adonis function) based on Bray-Curtis dissimilarities (with 999 permutations) to analyze the effects of plot type, sampling year, and their interaction on the taxonomic and functional composition of ant and spider communities. First, we created matrices that combined information on plot taxonomic and functional composition (for each sampling period). In the case of the taxonomic analysis, the matrix cell values reflected ant occurrence and spider abundance; in the case of the

functional analysis, they were the abundance-weighted trait values. Second, we ran models in which sampling year (continuous variable), plot type (categorical variable), and their interaction were included as explanatory variables, and plot identity was a random factor. Third, we used non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities to explore differences in the taxonomic and functional composition of communities among plots and years. The assumption that the data displayed homogeneity of dispersion was tested using the betadisper function in the *vegan* package (Oksanen et al., 2018). We also tested for correlations among traits using the Spearman method (cor function in the *stats* package). We considered that two traits were highly correlated when rho ≥ 0.9 .

3. Results

3.1. Taxonomic diversity and composition

We captured a total of 31,833 ant workers representing 37 species (Appendix D, Table D.1), 15 genera, and 3 subfamilies as well as 3,391 individual spiders representing 63 genera (Appendix D, Table D.2) and 25 families. The rarefaction curves were more asymptotic for the ants

Table 1

Statistical output of the linear and quadratic mixed-effects models analyzing the effects of fire (plot type: burned vs. unburned), sampling year (year and year²), and their interaction on occurrence, taxonomic richness (S), Shannon diversity (H), Pielou's evenness (J), log-transformed functional richness (log[FRic]), functional evenness (FEve), and functional dispersion (FDis) for the ant communities. -, indicates that the quadratic year term was not used in the linear models. The blank spaces correspond to the quadratic models that had a poor fit for a particular explanatory variable. In bold are the significant values for a given explanatory variable in a given model.

Ants									
Occurrence	Linear model				AIC	Quadratic model			
	DF	F-value	p-value	DF		F-value	p-value	AIC	
Fire	1,4	2.94	0.161		77.122	1,4	2.95	0.161	75.125
Year	1,16	2.08	0.168			1,14	3.11	0.099	
Year ²	-	-	-			1,14	7.15	0.018	
Fire \times Year	1,16	1.19	0.293			1,14	1.77	0.205	
Fire \times Year ²	-	-	-			1,14	2.72	0.121	
<i>Taxonomic richness (S)</i>									
Fire	1,4	31.00	0.005	124.965		1,4	34.68	0.004	121.514
Year	1,16	0.70	0.415			1,14	0.78	0.39	
Year ²	-	-	-			1,14	1.68	0.216	
Fire \times Year	1,16	2.28	0.151			1,14	2.55	0.133	
Fire \times Year ²	-	-	-			1,14	2.69	0.123	
<i>Shannon diversity (H)</i>									
Fire	1,4	19.63	0.011			-	-	-	
Year	1,16	3.35	0.086			-	-	-	
Year ²	-	-	-			-	-	-	
Fire \times Year	1,16	2.39	0.141			-	-	-	
Fire \times Year ²	-	-	-			-	-	-	
<i>Pielou's evenness (J)</i>									
Fire	1,4	1.54	0.281	-52.068		1,4	1.55	0.281	-36.344
Year	1,16	2.54	0.131			1,14	2.7	0.122	
Year ²	-	-	-			1,14	1.8	0.200	
Fire \times Year	1,16	0.24	0.629			1,14	0.26	0.619	
Fire \times Year ²	-	-	-			1,14	1.24	0.284	
<i>Functional richness (log[FRic])</i>									
Fire	1,4	12.4	0.024	134.164		1,4	12.27	0.025	131.999
Year	1,16	0.18	0.676			1,14	0.18	0.678	
Year ²	-	-	-			1,14	1.12	0.307	
Fire \times Year	1,16	0.07	0.791			1,14	0.07	0.792	
Fire \times Year ²	-	-	-			1,14	0.67	0.426	
<i>Functional evenness (FEve)</i>									
Fire	1,4	0.80	0.423			-	-	-	
Year	1,16	0.34	0.567			-	-	-	
Year ²	-	-	-			-	-	-	
Fire \times Year	1,16	0.02	0.896			-	-	-	
Fire \times Year ²	-	-	-			-	-	-	
<i>Functional dispersion (FDis)</i>									
Fire	1,4	1.77	0.254	-89.396		1,4	1.77	0.255	-67.133
Year	1,16	12.97	0.002			1,14	11.77	0.004	
Year ²	-	-	-			1,14	0.49	0.495	
Fire \times Year	1,16	7.56	0.014			1,14	6.87	0.020	
Fire \times Year ²	-	-	-			1,14	0.04	0.849	

than for the spiders (Appendix E, Fig. E.1a,d).

Ant occurrence was significantly related to year (but not to plot type); the relationship was U shaped (Table 1), with ant occurrence decreasing from 2009 to 2011 and then increasing from 2011 to 2012 (Fig. 1a). Meanwhile, ant richness (S) and diversity (H) differed significantly between plot types but not among years (Table 1); lower values were seen in the burned versus unburned plots (Fig. 1b-c). For spiders, diversity was significantly and linearly related to year (Table 1) and increased from 2009 to 2012 (Fig. 1f). The interaction between plot type and year was significant for spider abundance and richness (Table 1). In the unburned plots, both variables had constant intermediate values across years; in the burned plots, values were low in 2009 but reached high levels in 2012 (Fig. 1d,e). There were no differences in taxonomic evenness over time between plot types, nor was there a year-by-plot-type interaction for either ants or spiders (Tables 1 and 2). These results were echoed in the rarefaction curves, where, for ants, taxonomic richness and Shannon diversity values were higher in the unburned versus burned plots. In contrast, there was overlap in the curves for ant and spider taxonomic evenness and for spider taxonomic richness and Shannon diversity, meaning these variables did not differ between the burned and unburned plots (Appendix D, Fig.D.1).

For ants, there was a significant effect of plot type and sampling year on community species composition (PERMANOVA: plot type— $F = 10.3$, $p = 0.001$, $R^2 = 0.30$; sampling year— $F = 2.6$, $p = 0.001$, $R^2 = 0.08$; Fig. 2a), but the interaction between plot type and sampling year was not significant ($F = 0.98$, $p = 0.083$, Fig. 2a). The taxonomic composition of spider communities was significantly influenced by plot type ($F = 6.9$, $p = 0.001$, $R^2 = 0.21$), sampling year ($F = 5.1$, $p = 0.001$, $R^2 = 0.15$), and their interaction ($F = 1.5$, $p = 0.040$, $R^2 = 0.05$). The assumption of homogeneity of dispersion was met for both the ants ($p =$

0.124) and the spiders ($p = 0.329$). Community composition differed between burned and unburned plots and among sampling years for both taxa (Fig. 2a,b). In the unburned plots, we observed ant species that are associated with vegetated habitats (e.g., *Crematogaster scutellaris*, *Camponotus lateralis*, and several *Temnothorax* species) and spider genera or species that live in vegetation or under stones (e.g., *Saites barbipes*, *Cercidia prominens*, *Hahnia* sp., *Trabea* sp., *Zora* sp., *Paracletes* sp., *Dysdera* sp., and members of the Linyphiidae family). In contrast, in the burned plots, we observed ant species typically found in open areas (e.g., *Cataglyphis iberica*, *Iberoformica subrufa*, *Pheidole pallidula*, *Plagiolepis pygmaea*, and *Tetramorium semilaeve*) and spider genera or species typically found in dry, stony grasslands and along the edges of coniferous forests (e.g., *Synema globosum*, *Atypus affinis*, *Alopecosa* sp., *Pardosa* sp., *Euophrys* sp., *Zodarion* sp., *Eresus* sp., and *Nemesia* sp.) (Fig. 2a,b). Ant and spider communities differed between 2009 (immediately after the fire) and the other three years of the study. In 2009, we observed ant species such as *Iberoformica subrufa*, *Camponotus piceus*, *Plagiolepis pygmaea*, and *Tapinoma nigerrimum* and mainly spiders from the genus *Nemesia*.

3.2. Functional diversity and composition

None of the functional diversity indices for either the ants or spiders differed significantly between the burned and unburned plots, apart from functional richness (FRic) and functional dispersion (FDis) for ants (Table 1). Ant FRic was higher in the unburned plots than in the burned plots (Fig. 3a). Ant functional dispersion (FDis) was affected by the interaction between plot type and sampling year (Table 1): while it was high and constant across all years in the unburned plots, it climbed from low values in 2009 to high values (equivalent to those in unburned plots)

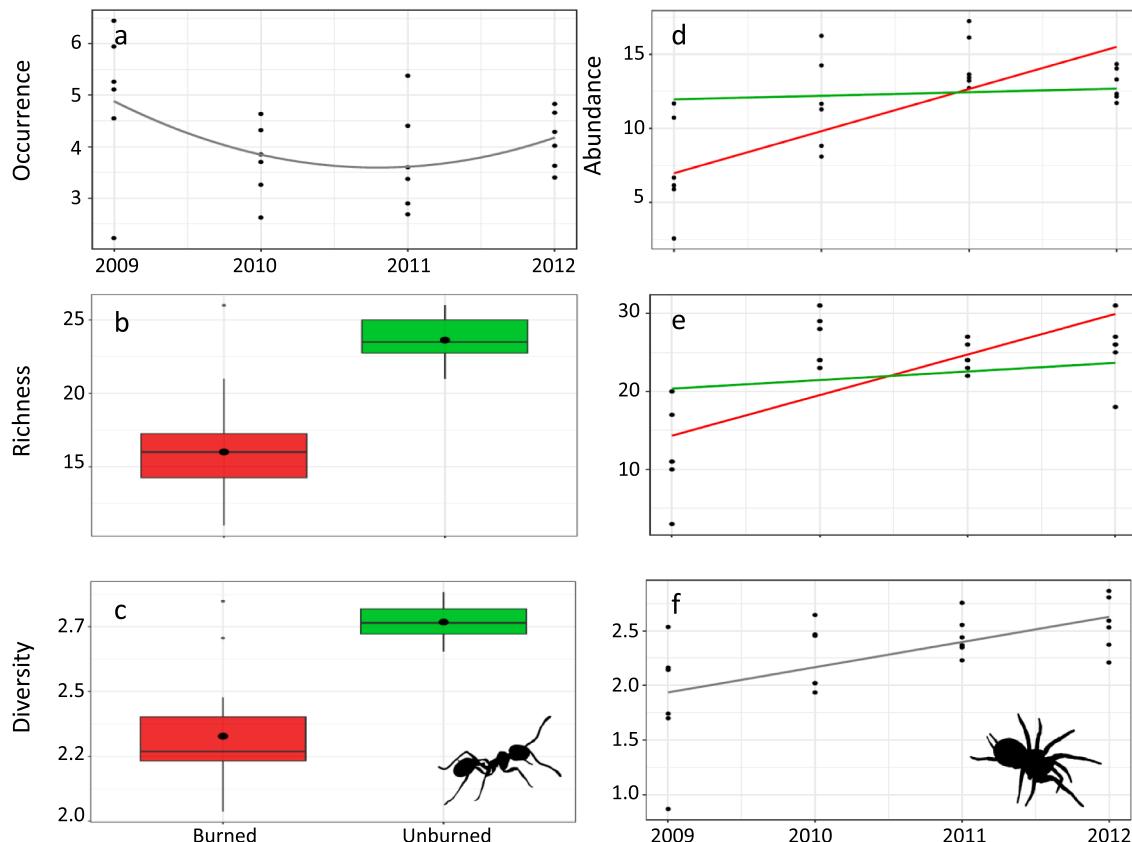


Fig. 1. Relationship between sampling year and ant occurrence (a) and mean (\pm SE) ant richness (b) and Shannon diversity (c) in burned versus unburned plots. Relationship between sampling year and plot type for spider square-root-transformed abundance (d) and richness (e) and the relationship between sampling year and spider diversity (f). The gray line indicates the linear or quadratic fit of the model, and the colors indicate the linear fit of the models for each plot type (red = burned; green = unburned).

Table 2

Statistical output of the linear mixed-effects and quadratic models analyzing the effects of fire (plot type: burned vs. unburned), sampling year (year and year²), and their interaction on square-root-transformed abundance, taxonomic richness (S), Shannon diversity (H), Pielou's evenness (J), functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis) for the spider communities. -, indicates that the quadratic year term was not used in the linear models. The blank spaces correspond to quadratic models that had a poor fit for a particular explanatory variable. In bold are the significant values for a given explanatory variable in a given model.

Spiders								
Abundance ^{1/2}	Linear model			AIC	Quadratic model			AIC
	DF	F-value	p-value		DF	F-value	p-value	
Fire	1,4	0.97	0.381	116.28	1,4	1.56	0.279	107.06
Year	1,16	18.04	<0.001		1,14	29.18	<0.001	
Year ²	-	-	-		1,14	12.82	0.003	
Fire × Year	1,16	6.95	0.018		1,14	11.24	0.005	
Fire × Year ²	-	-	-		1,14	1.53	0.237	
<i>Taxonomic richness (S)</i>								
Fire	1,4	0.00	0.961	147.29	1,4	0.00	0.955	132.596
Year	1,16	14.43	0.002		1,14	29.52	0.000	
Year ²	-	-	-		1,14	17.85	0.001	
Fire × Year	1,16	3.67	0.074		1,14	7.50	0.016	
Fire × Year ²	-	-	-		1,14	2.70	0.123	
<i>Shannon diversity (H)</i>								
Fire	1,4	6.19	0.068		-	-	-	
Year	1,16	21.96	0.000		-	-	-	
Year ²	-	-	-		-	-	-	
Fire × Year	1,16	5.52	0.032		-	-	-	
Fire × Year ²	-	-	-		-	-	-	
<i>Pielou's evenness (J)</i>								
Fire	1,4	6.06	0.070		-	-	-	
Year	1,16	0.30	0.594		-	-	-	
Year ²	-	-	-		-	-	-	
Fire × Year	1,16	0.00	0.987		-	-	-	
Fire × Year ²	-	-	-		-	-	-	
<i>Functional richness (FRic)</i>								
Fire	1,4	2.63	0.180	-0.971	1,4	3.41	0.139	5.545
Year	1,16	13.39	0.002		1,14	17.33	0.001	
Year ²	-	-	-		1,14	7.69	0.015	
Fire × Year	1,16	2.41	0.140		1,14	3.12	0.099	
Fire × Year ²	-	-	-		1,14	0.21	0.656	
<i>Functional evenness (FEve)</i>								
Fire	1,4	6.06	0.070		-	-	-	
Year	1,16	0.30	0.594		-	-	-	
Year ²	-	-	-		-	-	-	
Fire × Year	1,16	0.00	0.987		-	-	-	
Fire × Year ²	-	-	-		-	-	-	
<i>Functional dispersion (FDis)</i>								
Fire	1,4	1.05	0.364	-42.497	1,4	1.05	0.364	-39.794
Year	1,16	0.02	0.887		1,14	0.05	0.825	
Year ²	-	-	-		1,14	17.66	0.001	
Fire × Year	1,16	0.50	0.490		1,14	1.23	0.286	
Fire × Year ²	-	-	-		1,14	7.88	0.014	

in 2012 in the burned plots. (Fig. 3b). For the spiders, only FRic showed a significant linear increase across years (Table 2, Fig. 3c). There were no differences in spider functional evenness (FEve), spider functional dispersion (FDis), or ant functional evenness among years and between plot types. These variables were also unaffected by the year-by-plot-type interaction (Tables 1 and 2).

The functional composition of ant communities was affected by plot type, sampling year, and their interaction (PERMANOVA: plot type— $F = 1.6$, $p = 0.003$, $R^2 = 0.06$; sampling year— $F = 3.1$, $p = 0.003$, $R^2 = 0.12$; interaction— $F = 1.4$, $p = 0.020$, $R^2 = 0.05$, Fig. 4a). The functional composition of spider communities was also affected by plot type ($F = 5.7$, $p = 0.004$, $R^2 = 0.16$), sampling year ($F = 7.4$, $p = 0.004$, $R^2 = 0.20$), and their interaction ($F = 3.0$, $p = 0.014$, $R^2 = 0.08$) (Fig. 4b). The assumption of homogeneity of dispersion was met for both ants ($p = 0.08$) and spiders ($p = 0.302$). Similarly, the functional composition of ant and spider communities differed between plot types and among sampling years (Fig. 4a,b). In the unburned plots, we observed ant species that build their nests in the vegetation; that forage individually; and that consume a sugar-based diet. In the burned plots, we observed ant species that are predominantly diurnal; that consume insect- and seed-based diets; that forage collectively; and that display dependent

colony foundation, polydomy, and polygyny (Fig. 4a). In the unburned plots, we found spiders that are predominantly nocturnal and that hunt using webs. In the burned plots, we found spiders that are predominantly diurnal; that hunt using an ambush strategy; that excavate burrows; and that have specialized diets. We did not see a clear effect on body size distribution for either taxa. The functional composition of the spider communities in the burned plots differed between 2009 and the other three years of the study; in 2009, the burned plots were more similar to the unburned plots. Traits like ambush hunting and burrowing were more common in the burned plots in 2009 (Fig. 4).

We observed some strong correlations ($\rho \geq 0.9$) between the focal traits for both taxa (Appendix C: Tables C.3 and C.4). For the ants, it was interesting to note that dependent colony foundation (DCF) was negatively correlated with having an insect-based diet. Competitive dominance was positively correlated with collective foraging, worker polymorphism, and colony size. Moreover, colony size was correlated with collective foraging. Having a sugar-based diet was positively correlated with nesting in vegetation (Table C.3). In spiders, ballooning was positively correlated with active hunting and was negatively correlated with ambush hunting and burrowing. The length of time that females remained active was negatively correlated with being strictly

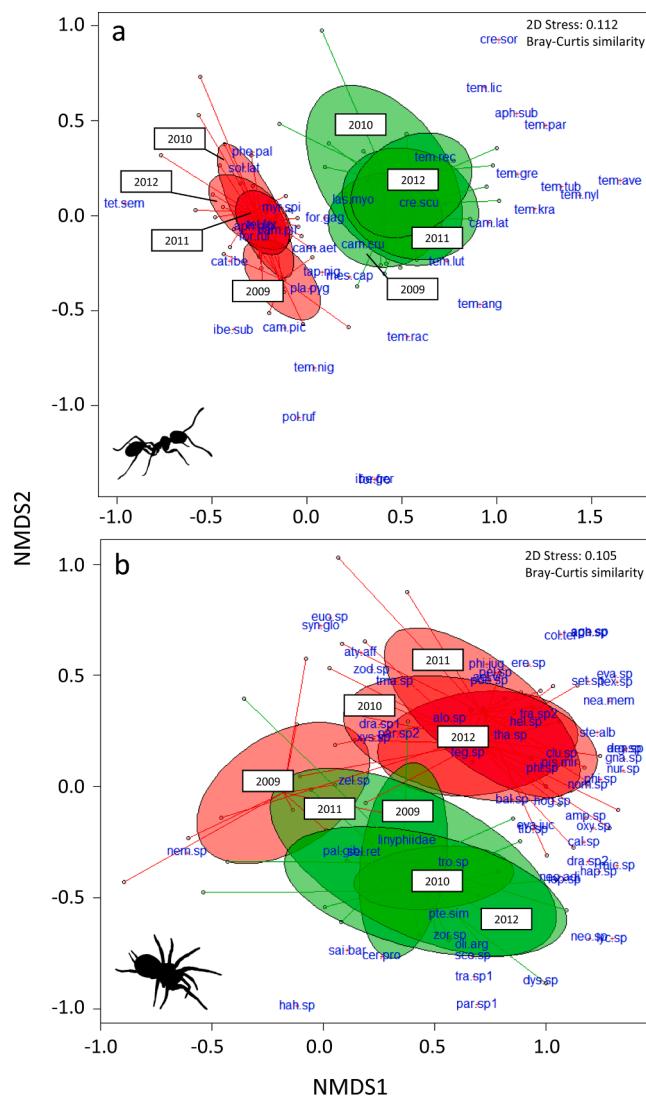


Fig. 2. Results of the NMDS analysis of community taxonomic composition for ants (a) and spiders (b). The ovals depict the standard deviation of the point scores and represent the different sampling years. The colors indicate plot type (red = burned; green = unburned).

diurnal and having a specialized diet. Active hunting was negatively correlated with burrowing. Ambush hunting was positively correlated with body size and burrowing. Both active and ambush hunting were negatively correlated with foraging for food on the ground. Finally, burrowing was positively correlated with body size.

4. Discussion

In this study, we examined the taxonomic and functional responses of both ant and spider communities to a wildfire that completely changed forest habitat conditions. We sampled immediately after the fire and over the subsequent four years. This longitudinal approach allowed us to clarify the patterns and mechanisms associated with the short-term survival, persistence, and colonization dynamics of two distinct taxa. This work is an important step in establishing a theoretical framework for understanding invertebrate responses to forest wildfires and for developing appropriate biodiversity monitoring strategies. We observed that although taxonomic and functional diversity displayed parallel responses to fire, such responses were also taxon specific. This result highlights the importance of approaching diversity from several perspectives and using different taxonomic groups, especially if the

ultimate objective is to inform conservation efforts.

Our first hypothesis predicted that the taxonomic and functional diversity of both ant and spider communities would decrease immediately after the fire and that the effect would be more dramatic for spiders than ants. This prediction was not supported by our results. Notably, several diversity indices did not differ between plot types for either group immediately after the fire. In fact, contrary to our expectations, the effects of fire were always more marked in ants than in spiders. More specifically, we found that ant FDis was lower after the fire but increased over the years. We also observed that fire negatively affected ant richness, diversity, and FRic but did not spider taxonomic and functional diversity in any form. Past research has revealed that arthropod taxonomic diversity can respond in a wide variety of ways to fire (review in Kral & al. 2017). Our results are similar to those seen in earlier studies, which found that fire had a weak effect on spider taxonomic diversity (Underwood and Quinn, 2010) and that the immediate taxonomic responses of spiders to fire were generally positive or neutral (Podgaiski et al., 2013). In contrast, in ants, the immediate taxonomic responses to fire can be neutral (Underwood and Quinn, 2010), positive (Andersen et al., 2014; Maravalhas and Vasconcelos, 2014), or negative (Punttila and Haila, 1996; Verble-Pearson and Yanoviak, 2014). This greater variability of responses might be due to differences in habitat type and plant species composition (Andersen, 2019) as well as in fire intensity, frequency, and/or severity. In our case, the sampling area was dominated by the sub-Mediterranean pine species *Pinus nigra*, a species that does not recover from crown wildfires (Rodrigo et al., 2004). As a result, the ants were negatively affected by the major environmental modifications that took place. Interestingly, the effects on taxonomic diversity translated into effects on functional diversity in ants. This result furnishes further evidence that strong linear relationships exist between taxonomic and functional diversity along successional gradients in forests, as previously observed in trees (Lohbeck et al., 2012) and in ants (Rocha-Ortega et al., 2018). It also provides support for the predictions of the niche complementarity hypothesis: the presence of more species should lead to the more exhaustive use of resources, resulting in higher rates of ecosystem functioning (Tilman et al., 1997). Whatever the case, we have demonstrated that ant communities are not necessarily more resistant than spider communities to fire.

Our second hypothesis predicted that the taxonomic and functional diversity of both the ant and spider communities would increase over time, with the spiders recovering more quickly than the ants. We found support for this hypothesis. While spider abundance and richness initially declined after the fire, both recovered within two years, a result that has been seen in other studies (Polchaninova et al., 2016; Vasconcelos et al., 2009). In ants, several taxonomic and functional variables were affected by fire (richness, diversity, Fric, and FDis) and did not recover over the four years of the study, with the exception of FDis. Past work suggests that dramatic variability exists in how well ant communities recover following a fire. Some studies have found that the taxonomic structure of ant communities can completely recover quite quickly (in 1–8 months; Parr et al., 2004; Verble-Pearson and Yanoviak, 2014) and that ants may even be among the first wave of colonizers following forest fires (Antunes et al., 2009). However, other studies have shown that ant community structure may not have recovered fully even 8 years later (Arnan et al., 2006). This variability may be shaped by forest type, which influences forest recovery dynamics (Arnan et al., 2006) and/or the ability of ants to persist under post-fire conditions (Parr et al., 2004). Following a fire, ant taxonomic and functional diversity may decrease because of changes in vegetation structure (Arnan et al., 2007), temperature (Arnan et al., 2014; Raymons et al., 2013), aridity (Arnan et al., 2018), resource availability (Lázaro-González et al., 2013), and the functional properties of soils (Antunes et al., 2009). Indeed, certain species in our study area—namely species that have strong associations with the vegetation (e.g., *Crematogaster scutellaris*, *Lasius myops*, and *Camponotus lateralilis*) and/or that have cryptic lifestyles (e.g., *Temnothorax* species)—cannot cope with the new

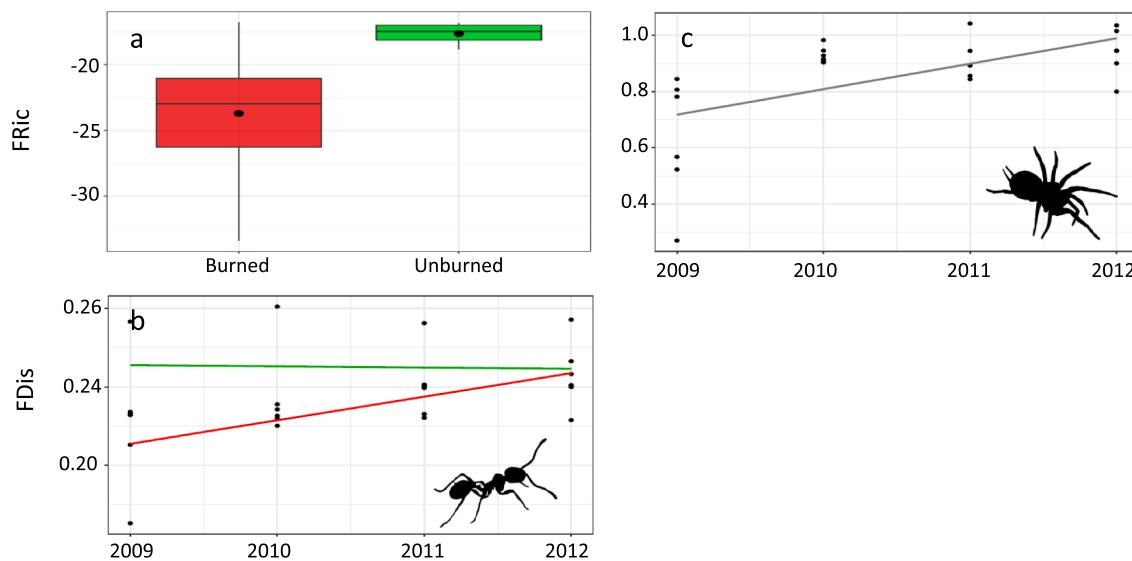


Fig. 3. Mean (\pm SE) log-transformed ant functional richness in burned versus unburned plots (a); the relationship between sampling year and ant functional dispersion; (b) and the relationship between sampling year and spider functional richness (c). The gray line indicates the linear fit of the model, and the colors indicate the linear fit of the models for each plot type (red = burned; green = unburned).

environmental conditions. More specifically, temperature and aridity climb as a result of post-fire conditions, as the cover previously provided by the tree canopy has disappeared. This situation can intensify the fire's negative effects and reduce the diversity of food acquisition strategies represented within the community (Arnan et al., 2018), thus impeding recovery. It is important to note that the practical constraints of sampling hinder replication. Indeed, it is often challenging to successfully implement a fully segregated sampling regime in fire ecology research (Parr and Chown, 2003). While this limitation might have reduced the statistical power of our models, our rarefaction curves suggest otherwise. They showed that ant taxonomic richness and Shannon diversity were higher for the two unburned plots than for the four burned plots, which indicates that our sampling efforts were sufficient to detect consistent differences between plot types.

Our third hypothesis predicted that the burned and unburned plots would contain different types of species displaying certain sets of traits. In the burned plots, we expected to see species more typically found in open areas, notably those that build their nests and search for food in/on the ground and that disperse longer distances. In the unburned plots, we expected to see species more typically associated with vegetated habitats, such as those that disperse shorter distances. Our results support this hypothesis: we found significant differences in the taxonomic and functional composition of ant and spider communities between the burned and unburned plots. Examining the species' traits more closely revealed more detailed patterns.

First, the likelihood of surviving the fire was enhanced by certain traits. Ants or spiders that nest in the ground or that excavate burrows (e.g., ants: *Pheidole pallidula*, *Tetramorium semilaeve*; spiders: *Atypus affinis*, *Eresus* sp.) (Antunes et al., 2009) had higher survival rates than species that live in close association with the vegetation (Matsuda et al., 2011). Indeed, in the burned plots, we less frequently observed ants that nest in the vegetation (e.g., *Crematogaster scutellaris* and several *Temnothorax* spp.) and spiders that use the vegetation when building webs or hunting (e.g., *Saites barbipes*, *Cercidia prominens*, *Hahnia* sp., and *Linyphiidae* spp.). Because they rely more heavily on the vegetation, tree-dwelling ants and spiders were more negatively affected by the fire (Moretti et al., 2002; Underwood and Quinn, 2010).

Second, persistence following the fire was enhanced by other traits. The survivors had to cope with warmer, drier, and structurally simplified habitats. Past work has shown that the surface upon which ants and spiders forage (e.g., the vegetation or the ground) and the type of food

resources they exploit can also influence species persistence (Arnan et al., 2007; Rodrigo and Retana, 2006). Consequently, we expected that species foraging on the vegetation would be more negatively affected by post-fire conditions. What we found was that species in the burned plots displayed certain dietary traits (insect- and seed-based diets in ants, specialized diets in spiders) and foraging/hunting strategies (collective foraging in ants and ambush hunting in spiders). The availability of different food resources can shift dramatically following fire (Arnan et al., 2007) because burned areas are more open, resulting in a greater abundance of dead insects (due to greater sun exposure) and seeds (from successional, herbaceous plants). It thus made sense that persistence levels were higher for ant species (e.g., *Iberoformica subrufa*, *Pheidole pallidula*, and *Tetramorium semilaeve*) that collectively forage upon these resources (Arnan et al., 2015; Retana et al., 1992). The two most abundant epigaeic spider genera in the burned plots were generalist insectivores and strict myrmecophages (*Pardosa* sp. and *Zodarion* sp., respectively), which is likely linked to the presence of ants in the plots. Post-fire conditions also favored the persistence of spiders that ambush their prey rather than using webs (e.g., *Synema globosum* and *Nemesia* sp.) since little to no vegetation was available for web building. In addition, the burned plots contained ants and spiders that are predominantly diurnal, probably because the thermophilic species in the two taxa are predominantly diurnal and prefer open habitats. In contrast, in the unburned plots, ants tended to be group foragers, and spiders tended to use web-based hunting. This pattern likely resulted because the unburned plots contained a large number of *Temnothorax* species, which all forage collectively. As for the spiders, they generally belonged to genera (or species) that build webs on the vegetation. In fact, some species in the ant genus *Temnothorax* and in the spider family Linyphiidae are commonly found in intact forests and serve as bioindicators of forest health (Moretti et al., 2002) because they are very sensitive to disturbance.

However, one facet of our third hypothesis was not supported because the burned plots did not contain ants and spiders capable of dispersing longer distances. The ant species observed in the burned plots use dependent colony foundation (DCF), a system in which a portion of a mature colony slowly disperses a short distance to found a new colony. This finding contrasts with that of Punttila and Haila (1996), who found that ants in burned areas utilized independent colony foundation (ICF). It is important to note, though, that their study was experimental, and they quantified the presence of founding queens in artificial nest sites

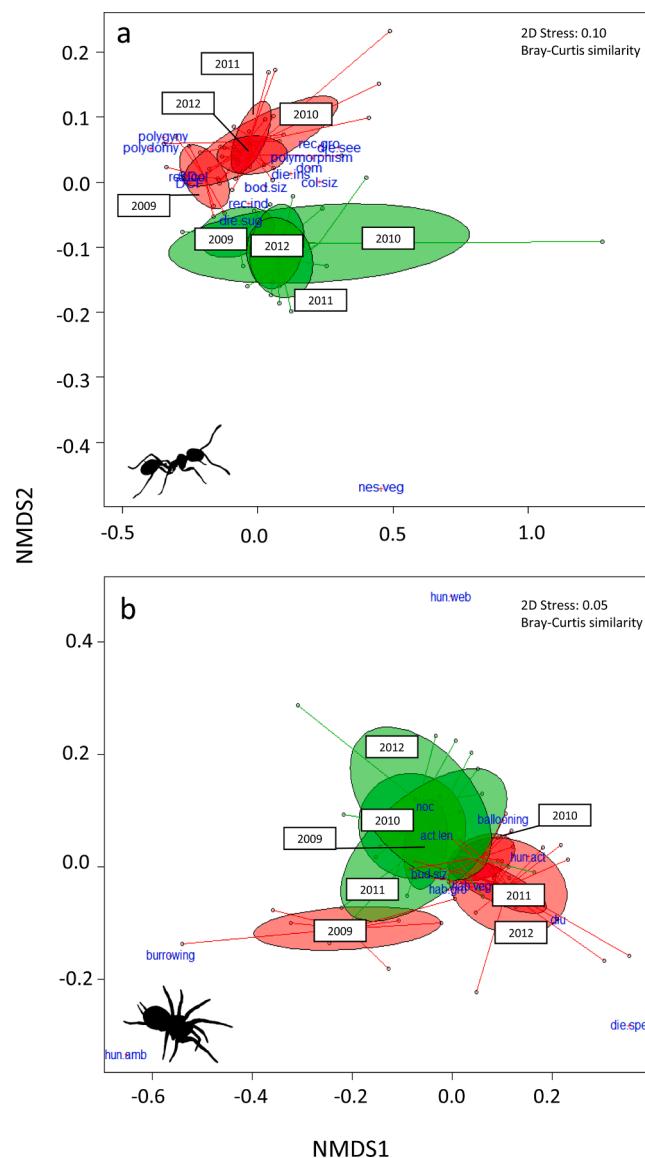


Fig. 4. Results of the NMDS analysis of community trait composition for ants (a) and spiders (b). The ovals depict the standard deviation of the point scores and represent the different sampling years. The colors indicate plot type (red = burned; green = unburned).

and stumps. In contrast, in our study, we indirectly identified colonizers based on worker presence in pitfall traps. This difference in methodologies could explain the difference in results because, in the first few years following nest foundation, ICF colonies have smaller numbers of foragers, while DCF colonies have larger numbers of foragers (between 1/3 to 1/4 of the number in the mother colony; Amor et al., 2011; Chéron et al., 2011). As a consequence, it would be harder to detect the presence of ICF species versus DCF species using pitfall trapping. Another factor to consider is the distance between the burned and unburned plots. In our study, this distance was not always very large, and the burned plots could thus have acted as reservoirs (Antunes et al., 2009). However, it is important to note that DCF was strongly and negatively correlated with having an insect-based diet, so we cannot know whether one or both traits were directly operated on by fire. It is possible that we did not find more ICF species in the burned plots simply because certain resources (e.g., liquid resources) were absent. In our study area, many of the ant species displaying ICF (62%) also have a sugar-based diet, which is largely composed of flower nectar and honeydew. Honeydew production is higher in forests than in open areas

because the aphids responsible for its production display higher yields when feeding on woody versus herbaceous plants (Dixon 1975). We also predicted that the burned plots would contain more species of spiders that use ballooning, a behavior whereby juveniles move through the air using silk threads (Bell et al., 2005). This dispersal strategy allows spiders to move longer distances. However, ballooning species were found in both the burned and the unburned plots, probably because this trait is displayed by the majority (63%) of the spider genera that we observed in our study area (Bell et al., 2005). It is also possible that the strong and negative correlation we found between ballooning and ambush hunting could have biased the ballooning results.

It is worthwhile to consider whether these responses to disturbance could influence ecosystem functioning. First, ecosystems can display functional resistance if a disturbance eliminates certain species, but remaining species and/or new species can serve the same functions as those that have disappeared. We observed that, in ants, both taxonomic and functional diversity were affected by fire; in spiders, in contrast, neither diversity type was dramatically affected. Second, ecosystems can display functional resilience if changes in community composition result in a new community that is functionally similar. Such was not the outcome in our study system: there were pronounced differences in the functional traits represented in the burned versus unburned plots (e.g., nesting site, foraging and hunting strategies, and diurnality). Overall, we discovered that there were major changes in the taxonomic composition of ant and spider communities that then translated into functional changes. Past research has highlighted that functional diversity has a greater influence than taxonomic diversity on ecosystem processes (Gagic et al., 2015). As a result, the functional changes we observed might have important consequences for ecosystem functioning.

5. Conclusions

We found that forest fire can affect both ant and spider communities and that the effect is greater on the former than the latter. The fire changed both community structure (taxonomic and functional diversity) and composition in ants. In contrast, it had little effect on the structure of spider communities, although it did impact their taxonomic and functional composition. In their responses to fire, ants were not more resistant than spiders, but spiders were more resilient than ants. However, the effects of fire were certainly taxon dependent. By conducting an analysis of taxonomic and functional diversity across taxa, we were able to clarify the biotic responses of major arthropod groups to disturbance and explore the mechanisms in operation over time (i.e., survival, persistence, and colonization). Furthermore, we identified traits that allow species to better survive, persist, and colonize. We can use this information to analyze the functional composition of communities and then predict their responses to fire. We call for more long-term studies that will further enhance our knowledge in this area. Such research will greatly improve our ability to predict ecosystem responses, manage biodiversity, and implement conservation programs in the face of global changes.

CRediT authorship contribution statement

J. Manuel Vidal-Cordero: Formal analysis, Data curation, Visualization, Writing – original draft. **Xavier Arnan:** Conceptualization, Funding acquisition, Methodology, Investigation, Writing – review & editing. **Anselm Rodrigo:** Conceptualization, Funding acquisition, Methodology, Investigation, Writing – review & editing. **Xim Cerdá:** Conceptualization, Funding acquisition, Methodology, Investigation, Writing – review & editing. **Raphaël Boulay:** Conceptualization, Funding acquisition, Methodology, Investigation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank Íñigo Sánchez (Zoobotánico de Jerez) and Jesús Miñano (University of Murcia) for helping identify the spiders and for providing information on spider life-history traits; Xavier Espadaler (UAB), Alberto Tinaut (University of Granada), and Joaquín L. Reyes-López (University of Córdoba) for helping identify the ants and for providing information on ant life-history traits; and David Aragónés along with the rest of the EBD GIS and Remote Sensing Laboratory (LAST-EBD) for helping us create the maps. Jessica Pearce-Duvet provided English editing and useful comments. Alba Lázaro, Ana Carvajal, Anna Torné, Anna Revoltós, María Alba Recasens, Sergio Osorio, José Luis Ordóñez, Mike Jowers, Stéphane Caut, and Jessica Pearce-Duvet assisted with the pitfall sampling. Helena Barril contributed to the fieldwork; she also sorted and identified most of the ants. This study was funded by the Spanish Ministry of Science and Innovation (Consolider MONTES project, CSD 2008-00040). JMVC was supported by the La Caixa Foundation (ID 100010434 - agreement LCF/BQ/SO14/52250015); a project grant (RNM 2705, Proyectos de Excelencia, 2012) from the regional government of Andalucía (Consejería de Economía, Innovación, Ciencia y Empleo); and a project grant (CILIFO, reference: 0753_CILIFO_5_E) from the European Regional Development Fund (Interreg V A Spain – Portugal program [POCTEP]). XA was supported by a Ramón y Cajal research fellowship from the Spanish Ministry of Economy and Competitiveness (RYC-2015-18448). We thank two anonymous reviewers for their helpful and constructive comments on the manuscript and to Llorenç Badiella (Servei d'Estadística Aplicada, UAB) and José Luis Ruiz (López Neyra Institute of Parasitology and Biomedicine-CSIC) for their statistical advice.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120379>.

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