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Response of ant functional composition to fire

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Little is known about the impact of disturbances on functional diversity and the long-term provisioning of ecosystem services, especially in animals. In this work we analyze the effect of wildfire on the functional composition of Mediterranean ant communities. In particular, we asked whether a) fire changes functional composition (mean and dissimilarity of trait values) at the community level; and b) such fire-induced functional modification is driven by changes in the relative abundance-dominance of species or by a replacement of species with different traits. We sampled ant communities in burned and unburned plots along 22 sites in a western Mediterranean region, and we computed two complementary functional trait composition indices ('trait average' and 'trait dissimilarity') for 12 functional traits (related to resource exploitation, social structure and reproduction) and with two different datasets varying in the way species abundance is considered (i.e. abundance and occurrence data). Our results suggest a set of functional responses that seem to be related to direct mortality by fire as well as to indirect fire-induced modifications in environmental conditions relevant for ants. Trait average of colony size, worker size, worker polymorphism and the ratio between queen and worker size, as well as the trait dissimilarity of the proportion of behaviorally dominant species and of liquid food consumption, and overall functional diversity, were higher in burned than in unburned areas. Interestingly, different patterns arise when comparing results from abundance and occurrence data. While the response to fire in trait averages is quite similar, in the case of trait dissimilarity, the higher values in response to fire are much more marked when considering occurrence rather than abundance data. Our results suggest that changes in trait average are driven at the same time by replacement of species with different traits and by changes in the relative abundance-dominance of species, while fire promotes a higher diversity of functions that is primarily driven by rare species that are functionally unique. Overall, we observed major fire-induced changes in functional composition in Mediterranean ant communities that might have relevant consequences for ecosystem processes and services.

During the last decade functional diversity has become an important descriptor of species assemblages because it can show the impact of disturbances (de Bello et al. 2006, McGill et al. 2006, Laliberté et al. 2010) or identify ecological gradients (Mouillot et al. 2007, Swenson and Weiser 2010), while in turn it is an indicator of ecosystem function (Díaz and Cabido 2001, Petchey et al. 2004, Díaz et al. 2007). Measures of community functional composition and diversity tend to correlate more strongly than those of traditional species-diversity with ecosystem functions (Díaz and Cabido 2001, Petchey et al. 2004). While most studies addressing functional composition have been carried out on plants (Díaz et al. 2007), little is known about functional composition changes in animal communities in response to environmental factors.

Fire is one of the most important natural disturbances, especially in Mediterranean regions, and plays a key role in the dynamics and structure of plant and animal communities (diCastri and Mooney 1973, Naveh 1975, Gill et al. 1981). The number and extent of wildfires have increased in recent decades (Piñol et al. 1998, Carmo et al. 2011), and global predictions indicate a general increase in fire risk in the Mediterranean region due to current warming (Moriondo et al. 2006). It is thus of great interest to analyze the effects of fire on biodiversity and ecosystem function. Although responses to fire by animal communities are taxon-dependent, at a regional level fires usually benefit typical open-habitat species to the detriment of forest-specialist species (Swengel 2001, Schowalter 2012).

Ants are crucial components of most terrestrial ecosystems, contributing significantly to animal biomass and modifying the abiotic and biotic properties of their environment by performing a variety of ecological functions (Hölldobler and Wilson 1990, Folgarait 1998). The study of the effects of a wide range of disturbances on ant diversity has therefore aroused keen interest (Castaño-Meneses and Palacios-Vargas 2003, Arnan et al. 2006, 2009, Bihn et al. 2010). However, the vast majority of these works refer to taxonomic diversity, and very few to functional diversity (Bihn et al. 2010). There is a very substantial literature on the effects of fires on the structure and composition of ant communities at the taxonomic level (Parr et al. 2004, Arnan et al. 2006, Rodrigo and Retana 2006, Andersen et al. 2007, Frizzo et al. 2012), but as far we know, no study has analyzed it at the functional level (except for the functional group approach commonly used in Australian ant assemblages: Hoffman and Andersen 2003, Andersen et al. 2007). The fact that most studies reported that ant composition is widely modified by fire (Castaño-Meneses and Palacios-Vargas 2003, Parr et al. 2004, Arnan et al. 2006) suggests that wildfires could be a major driver of changes in ant functional diversity. Otherwise, species turnover should occur among functionally similar species (Moretti et al. 2009).

Direct and indirect functional responses to fire might be expected in ant communities. Fire directly causes the death of ants that nest in vegetation. However, most ground-dwelling species survive fire because temperature difference is negligible at a few cm below the ground surface (DeBano 2000, Arnan et al. 2006, Frizzo et al. 2012). Moreover, fire-induced modifications in vegetation physiognomy and composition also involve indirect relevant consequences on ground-dwelling ants in the mid- and long-term (Arnan et al. 2006, Rodrigo and Retana 2006). For instance, the suppression of vegetation cover by fire may increase ground temperature and limit habitat use by non-thermophilic ants (Andersen 1990, 1991, Boulay et al. 2009), thus selecting for heat-tolerance traits. Changes in temperature might also modify behavioral dominance in Mediterranean ecosystems (Retana and Cerdá 2000), with subordinates being favored in burned areas compared with behavioral dominants. Additionally, the modification of plant composition may also affect the availability of food resources such as seeds, nectar, aphid honeydew and corpses of herbivorous insects (Rodrigo and Retana 2006, Arnan et al. 2007a), thus modifying the proportion of different trophic guilds.

Variation in functional trait composition has often been described quantitatively by calculating indices based on either species abundance or species occurrence (Petchey and Gaston 2006, Villéger et al. 2008). The use of species abundance or species occurrence can lead to markedly different results and interpretations (de Bello et al. 2007). On the one hand, changes in functional composition that arise from abundance data are driven mostly by changes in the relative abundance-dominance of species. On the other hand, the changes that only arise from occurrence data indicate a replacement of species with different traits (de Bello et al. 2007). Therefore, complementary information provided from datasets with a different consideration of abundance might contribute to a better understanding of functional responses to disturbance at the community level.

In this paper we aim to analyze the functional response of ants to fire in the Mediterranean region. We considered twelve functional traits belonging to three traits groups (resource exploitation, social structure and reproduction) that account for different important components of ant colony's life which impact fitness indirectly via their effects on performance traits. We addressed the following questions: a) does fire favor different functional traits (mean and dissimilarity of trait values) at the community level? Assessing the trend that each functional trait follows after fire will determine which traits characterize species in burned and unburned areas; b) in the case of fire-induced modification of functional composition, is it driven by changes in the relative abundance-dominance of species or by a replacement of species with different traits?; and c) if there is a replacement of species with different traits, is such a substitution mainly related to rare species that might be characterized by unique traits (Bihn et al. 2010), or is it related to both dominant and rare species?

Material and methods

Study area

Fieldwork was conducted in 2002 in Catalonia (north-east Spain) in 22 sites (from ~ 0°18′–3°8′N to ~ 40°40′–2°24′W) burned in 1994 with canopy fire (Fig. 1). The study sites are described in detail in Arnan et al. (2006). In order to account for wide variability in Mediterranean post-fire vegetation recovery patterns (Rodrigo et al. 2004, Arnan et al. 2007b) and to account for general patterns, sites were distributed across eight vegetation types that were characterized by tree or shrub species with different post-fire response: shrubland dominated by seeders, shrubland dominated by resprouters, *Pinus halepensis* forest with tree understory, *Pinus halepensis* forest without tree understory, *Pinus nigra* forest, *Quercus ilex* forest, *Quercus suber* forest and *Fagus sylvatica* forest. We had three sites per vegetation type, except the beech forest, with only one replicate. Generally speaking, the % cover of the main tree or shrub species of burned plots was more similar to that of the unburned plots in the shrublands, the *P. halepensis* forests and the *Q. suber* forests, and less so in the *P. nigra* forests and *F. sylvatica* forests, while *Q. ilex* forests accounted for intermediate values; herbaceous and shrub cover was generally similar or higher in the burned than in the unburned areas, while tree cover was drastically lower in burned sites (Supplementary material Appendix 1; see also Arnan et al. 2006, 2007b). None of these areas was exposed to post-fire management practices (thinning or grazing) from 1994 to 2002.

Ant sampling

Five pairs of plots were placed in each site. One plot of each pair was located in the burned area, and the second plot was placed in the unburned area. This represented a total of 220 plots. All plots were located at > 100 m from the limit of the fire (either inside or outside), so that the distance between plots of each pair was < 200 m. Distance between paired plots within each site ranged from 30 to 5600 m. At each plot we established a 5 × 2 grid of pitfalls with 5 m spacing. This resulted in 10 traps per plot. Pitfall traps were 6.5 cm in diameter, 9.5 cm deep, plastic vials partially filled with water, ethanol and soap. Traps were operated during two contrasting periods within the usual activity period of most Mediterranean ant species (Cros et al. 1997): in mid-May (spring period) and in mid-July (summer period). In each sampling period, traps were operated for 7 d. The contents

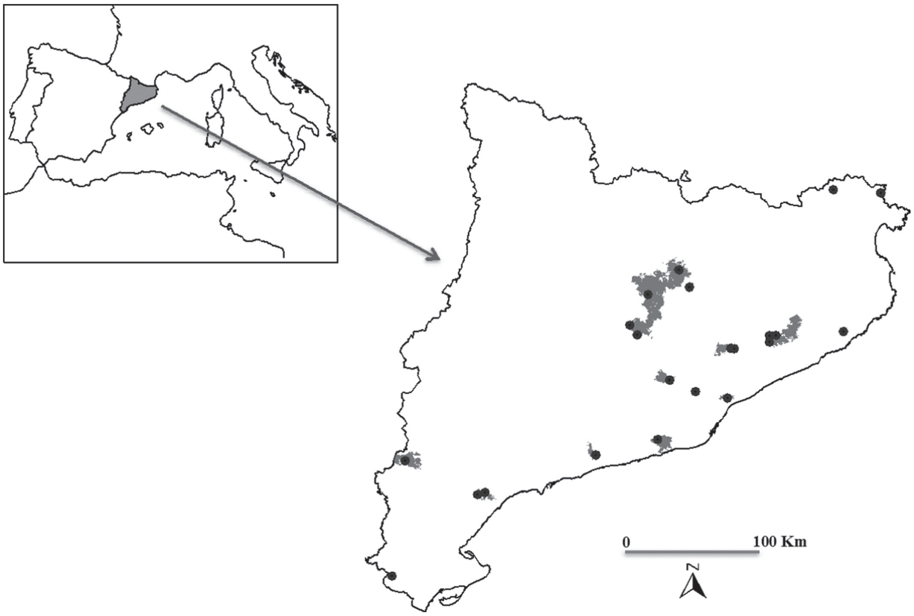

Figure 1. Map of Catalonia indicating the fires sampled (in grey) and the 22 study sites (black dots).

of the 10 traps of each plot were lumped together to obtain a single sample per plot (i.e. total number of ants per 10 traps over 7 d). Ants were sorted in the laboratory and identified to the species level. For further details of ant sampling see Arnan et al. 2006.

Ant species traits

Each species was described in terms of 12 functional traits belonging to three trait groups (Table 1) that are recognized as important in ant autoecology and/or that relate to ecosystem functioning (Hölldobler and Wilson 1990, Bihn et al. 2010, Lach et al. 2010). Functional traits were assumed to be species-specific without inter-site or inter-treatment (burned/unburned) variability (Swenson and Weiser 2010, Arnan et al. 2012). The omission of this variation probably results in an underestimation of the response of communities to environmental changes (Lepš et al. 2011), but the short time elapsed after the disturbance considered in this study suggests that it does not allow enough evolutionary time to produce intra-specific differences between colonies from

Table 1. Description of the ant functional traits used in this study. Traits were described for each species according to published sources or researcher expertise (where published information for a particular species was not available).

Ant trait group	Trait	Data type	States	Range
Social structure	Colony size	Quantitative	Number of workers per colony	50–150 000
	Number of queens	Ordinal	(0) Monogyny (0.5) Both monogyny and polygyny (1) Polygyny	0, 0.5, 1
	Number of nests	Ordinal	(0) Monodomy (0.5) Both monodomy and polydomy (1) Polydomy	0, 0.5, 1
Resource exploitation	Worker size	Quantitative	Worker body size from tip of mandibles to tip of gaster (mm)	1.6–10
	Worker polymorphism	Quantitative	Mean worker size divided by range worker size	0.1–1.1
	Diurnality	Binary	(0) Non-strictly diurnal (1) Strictly diurnal	0, 1
	Behavioral dominance	Binary	(0) Subordinate (1) Dominant	0, 1
	Diet – seed-eating	Fuzzy-coded*	0–1	0–1
	Diet – insect-eating	Fuzzy-coded*	0–1	0–1
	Diet – liquid food-eating	Fuzzy-coded*	0–1	0–1
Reproduction	Ratio queen/worker size	Quantitative	Mean queen size divided by mean worker size	1.1–2.8
	Colony foundation type	Ordinal	(0) Dependent Colony Foundation (DCF) (0.5) Both DCF and ICF; (1) Independent colony foundation (ICF)	0, 0.5, 1

*Diet categories were organized using a fuzzy-coding technique. Scores ranged from '0' (no preference for a food resource) to '1' (high preference for a food resource). This technique allowed considering within-species variability in diet. For instance, a species that mostly feeds on seeds and less on insects would be given an affinity of 0.75 for the seed-eating category, and a 0.25 for the insect-eating category.

unburned and burned areas. The first group of traits is composed of traits related to social structure, such as colony size, number of queens per colony (only one queen – monogyny-, more than one queen – polygyny, or both) and number of nests per colony (only one nest – monodomy-, more than one nest – polydomy-, or both). The second group is characterized by traits that are related to the ability of species to exploit food resources, such as worker size, worker polymorphism, the period of activity (non-strictly diurnal or strictly diurnal), position in the behavioral dominance hierarchy (behavioral dominant or subordinate) according to interspecific interactions at artificial food resources (i.e. baits), and the kind of food resource they exploit, i.e. to what extent they feed on seeds, insects or liquid food (nectar and/or honeydew). The third group of traits is composed of two life traits that relate to reproduction, the ratio between queen and worker size and the type of colony founding. Note that particularly the resource exploitation set of traits directly relates to impact on ecosystem functioning. Meanwhile, those traits grouped in social structure and reproduction are life-history traits that relate to ant autoecology and, although so far unknown, might have important implications for ecosystem function.

Information was first obtained from personal data and from personal communications from various colleagues (Anna Alsina, Jordi Bosch, Raphaël Boulay, Soledad Carpintero, Valentín Cavia, Sebastià Cros, Xavier Espadaler, Paqui Ruano and Alberto Tinaut), and was later complemented with an exhaustive search in public databases and scientific literature. A full list of the trait data sources used for this study is provided in Supplementary material Appendix 2.

Data analyses

Data analyses were conducted at the site level because the analyses of some traits, especially the binary and ordinal, were difficult to carry out at the plot level due to the low species number in some plots, which frequently generated null variability. Moreover, by using this procedure we diminished the weight of some accidentally highly abundant species at the plot level, due to the proximity between a pitfall trap and an ant nest. Ant abundance was then averaged among the five unburned and five burned plots of each site, and we obtained two paired samples of ant species composition (unburned and burned) per site. Since we were interested in general rather than seasonal patterns, the samples of the two sampling periods from each plot were pooled for analyses, so that we had one sample for the whole activity period of the ants. We agree that some seasonal functional patterns might be missed.

A variety of measures have been proposed to summarize variations in functional trait composition in a given community (Petchey and Gaston 2006, Villéger et al. 2008, Ricotta and Moretti 2011). These variations have often been quantified using two traditional indices which have been widely used in ecological research: the 'trait average', which provides an indication of the most common traits in a community, and the 'trait dissimilarity' (FD), which indicates to what extent the species within a community are different in their traits (Lepš et al. 2006, de Bello et al. 2007, Díaz et al. 2007, Petchey et al. 2007, Moretti et al. 2009, Ricotta and Moretti 2011).

The trait average for each site was computed as:

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

where p_i is the relative abundance of species i (for the species occurrence data, p_i is 1 divided by the number of species in that sample), and x_i is the trait value for species i.

When considering abundance data, this metric corresponds to the 'community-weighted mean' (CWM) (Ricotta and Moretti 2011) and is often understood as defining the dominant traits in a community. This relates to the 'mass ratio hypothesis' (Grime 1998), which holds that ecosystem functioning is largely controlled in the short term by dominant species (i.e. the most abundant species).

The FD index was computed as the Rao quadratic diversity index, which reflects the probability that two randomly picked individuals in a community will be different:

$$FD = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij}\, p_i\, p_j$$

where d_{ij} expresses the dissimilarity between each pair of species i and j, and p_i and p_j their relative abundance. The Rao coefficient presents several desirable properties for describing the functional diversity of a community (Botta-Dukát 2005, Ricotta 2005). We have chosen this index because it allows us to compute not only functional diversity for one single trait, but also for a combination of traits (Lepš et al. 2006), and can be handled for quantitative, categorical and binary traits. Raos's Q is relatively unaffected by species richness, and it ranges from 0 to the maximum Simpson index of diversity, with higher values indicating more trait community dissimilarity.

These indices were computed with R (R Development Core Team) using the dbFD function implemented in the FD library. Trait average was computed for each functional trait, while trait dissimilarity for each functional trait, each of the three groups of functional traits, and for all functional traits together (Table 1). Trait average and dissimilarity might provide similar information and might not be fully independent in the case of categorical traits (Ricotta and Moretti 2011). As we confirmed this pattern with our data (trait average and dissimilarity for most categorical traits were highly correlated, $r > 0.07$; Supplementary material Appendix 3), we conducted further analyses using only the trait dissimilarity for diurnality, dominance, number of queens, number of nests and colony foundation type). For the remaining continuous and fuzzy-coded variables, we also did correlations between the trait average and dissimilarity; they were only highly correlated for the % of seeds in diet (Supplementary material Appendix 3), and we then discarded the trait average for further analyses.

All these computations were applied to both abundance and occurrence data. Following the calculation for each site, we used general mixed linear models (GLMM) to test the effect of fire on functional trait composition indices

($\bar{X}$ and *FD*). Habitat type (burned or unburned) was the fixed factor, while site was treated as random in order to consider the burned and unburned areas of one site as spatial repeated measures. GLMMs were carried out using the function lme of the nlme package in R. When required, variables were transformed to match homoscedasticity. Since we conducted multiple tests, we applied the sequential Bonferroni correction separately for the trait average and dissimilarity analyses.

While specific trade-offs among plant traits are well known, little is known in animals, and even less in insects. Since we do not know about ant traits dependency at the specific level, patterns at community level might arise from trade-offs at the species level. Then, in order to be conservative and check for trade-offs among functional traits at the community level, we carried out Spearman rank correlations among the computed trait averages and among the dissimilarity values. But note that correlations between traits at the community level do not necessarily imply correlation at the species level (Ackerly et al. 2002).

In order to analyze if a replacement of species is driven by rare species or by both dominant and rare species, species were then divided into two classes, according to their abundance in the whole data set: dominants > 0.5% (16 species, 3–13 species per site) and rares < 0.5% (32 species, 4–16 species per site). After computing the same functional indices that we did with the whole community using these two new data subsets, we calculated the Spearman rank correlation between the indices (of each trait and groups of traits) computed for the whole community and those computed when considering only dominant or rare species. In order to analyze if dominant and rare species differed in trait composition, and then if rare species had unique combination of traits, we also computed correlations between functional indices (of each trait and group of traits) computed from dominant and rare species.

Results

We collected 234 398 ant workers belonging to 50 species and 18 genera. One temporary parasitic species (*Lasius affinis*) and one slave-making species (*Polyergus rufescens*) were removed for our functional analyses because they are exceptional cases and some of our functional traits (especially those traits related to resource exploitation) would not correspond to them, but to their host species. Ant species covered a wide range of values for the functional traits measured (Table 1).

Trait average

Fire significantly affected the trait average for three out of six functional traits, when taking into consideration both abundance and occurrence data (Table 2). Colony size and worker polymorphism were higher in burned than in unburned areas for both abundance and occurrence data. Moreover, burned sites were characterized by a higher queen/worker size when considering abundance data, and by larger workers when considering occurrence (Fig. 2). Trait averages of colony size and ratio of queen and worker size, as well as of worker size and worker polymorphism were highly correlated (Supplementary material Appendix 4).

Trait dissimilarity (FD)

When considering abundance data, no functional trait significantly differed in dissimilarity between the unburned and burned areas (Table 3). When considering occurrence data, the functional diversity of two single traits significantly changed due to fire (Table 3). Thus, dissimilarity in the degree of behavioral dominance and liquid food consumption was higher in burned areas (Fig. 2). Functional diversity of the combination of all traits and those related to resource exploitation was changed by fire, so that there was greater overall FD (mean ± SE = 0.05 ± 0.00 and 0.06 ± 0.00, respectively) and diversity of resource exploitation strategies (0.06 ± 0.00 and 0.07 ± 0.00, respectively) in burned than in unburned plots. There was a high correlation among trait dissimilarity of all traits together, resource exploitation traits and proportion of liquid food in diet (Supplementary material Appendix 5).

Relationship between the whole community patterns and those from only dominant and rare species

The community trait average of the six functional traits computed from the abundance of the whole community were highly correlated (r > 0.7) to those computed when considering only dominant species, while none was highly correlated

Table 2. Statistical outputs of GLMMs tests of effects of fire on the trait averages computed from each of the 12 functional traits on abundance and occurrence data. In bold, significant values after the sequential Bonferroni correction.

	Abundance data			Occurrence data		
Trait	Value ± SE	*t*-value	p	Value ± SE	*t*-value	p
Social structure						
Colony size	0.08 ± 0.02	4.30	**0.0003**	0.05 ± 0.01	5.61	**< 0.0001**
Resource exploitation						
Worker size	−0.03 ± 0.04	−0.68	0.5063	0.07 ± 0.02	3.94	**0.0007**
Worker polymorphism	0.11 ± 0.02	4.11	**0.0005**	0.04 ± 0.01	4.67	**0.0001**
Diet – insect-eating	−0.04 ± 0.03	−1.53	0.1397	−0.03 ± 0.01	−2.61	0.0164
Diet – liquid food-eating	−0.04 ± 0.03	−1.29	0.2125	−0.01 ± 0.01	−0.66	0.5151
Reproduction						
Ratio queen/worker size	0.13 ± 0.04	2.97	**0.0073**	0.01 ± 0.00	2.00	0.0583

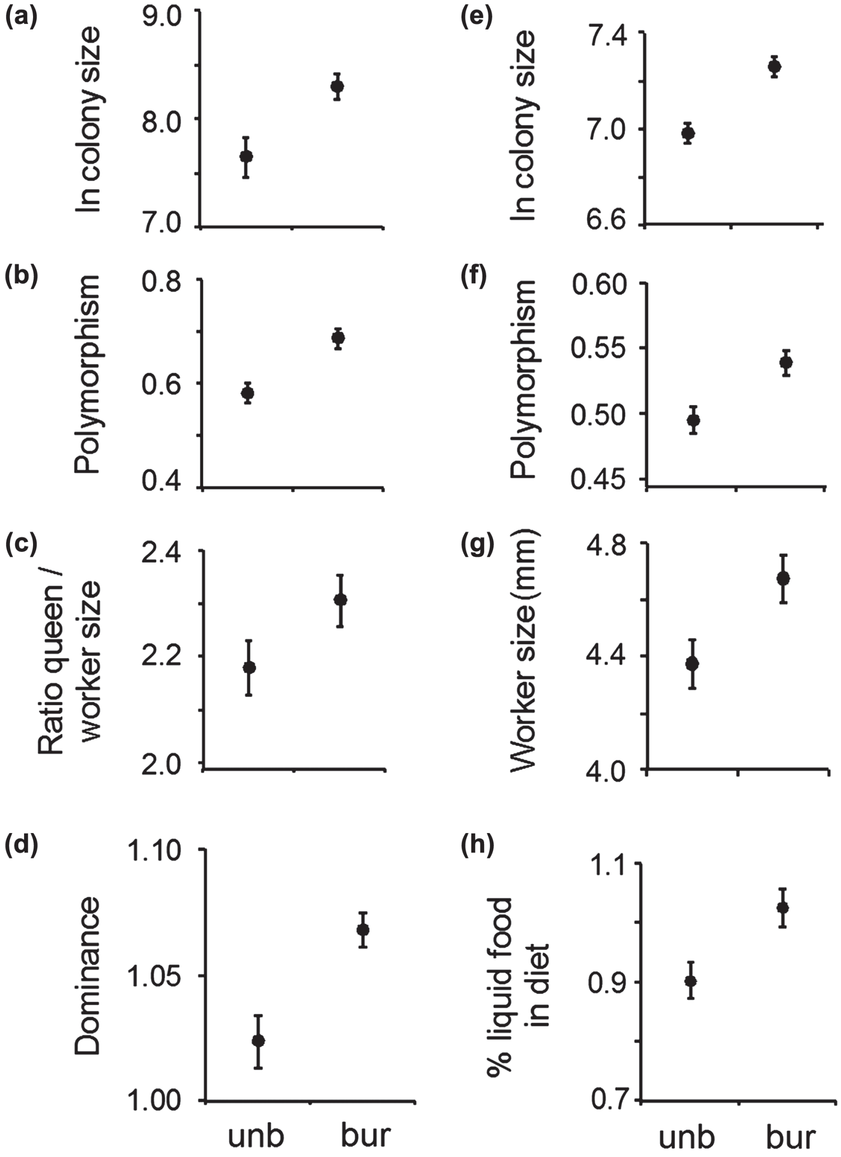

Figure 2. Mean (± SE) values of the trait average computed with abundance (a–c) and occurrence (e–g) data, and of the trait dissimilarity computed with occurrence data (d, h) for those single functional traits that significantly differed between unburned (UNB) and burned (BUR) sites.

to rare species (Table 4). On the contrary, when considering the occurrence dataset, trait average of the whole community was highly correlated to that of dominant species for only one trait, but six trait averages correlated to those of rare species (Table 4). No high correlations were found between trait average of dominant and rare species computed from both abundance and occurrence data sets.

There was also high correlation ($r > 0.7$) of the FD of all the sixteen functional traits (or groups of traits) computed from the abundance of the whole community to those computed when considering only dominant species, while none was highly correlated to rare species (Table 4). When taking into account the occurrence dataset, the trait dissimilarity of 6 and 11 traits of the whole community highly correlated to dominant and rare species, respectively (Table 4). Only one high correlation was found between the trait dissimilarity of dominant and rare species computed from both abundance and occurrence data sets.

Discussion

Our findings strongly indicate that fire modifies functional composition in the midterm in Mediterranean ant communities. Our study was conducted across a set of various typically Mediterranean vegetation types with different post-fire recovery patterns (Rodrigo et al. 2004, Arnan et al. 2007a, b), from plant communities with low or nil resilience to plant communities with medium-high resilience to fire at mid-term. Beyond the major changes due to fire in ant species composition that have been extensively reported in different regions (Farji-Brener et al. 2002, Castaño-Meneses and Palacios-Vargas 2003, Parr et al. 2004, Ratchford et al. 2005, Rodrigo and Retana 2006, Matsuda et al. 2011), and even in the study area (Arnan et al. 2006), this is the first study to report relevant changes in ant functional composition after wildfire from a trait-based approach. These effects were found for both trait average and dissimilarity.

Table 3. Statistical outputs of GLMMs tests of effects of fire on functional diversity based on RaoQ index values computed from each of the 12 functional traits, combination of different traits and all together on abundance and occurrence data. In bold, significant values after the sequential Bonferroni correction.

	Abundance data			Occurrence data		
Trait	Value ± SE	*t*-value	p	Value ± SE	*t*-value	p
Social structure	−0.02 ± 0.01	−1.27	0.2185	0.00 ± 0.01	0.77	0.4522
Colony size	−0.05 ± 0.04	−1.41	0.1721	−0.05 ± 0.03	−1.69	0.1053
Number of queens	−0.02 ± 0.06	−0.31	0.7587	0.13 ± 0.06	2.22	0.0377
Number of nests	−0.07 ± 0.06	−1.29	0.2118	0.16 ± 0.07	2.43	0.0244
Resource exploitation	0.01 ± 0.01	0.64	0.5304	0.01 ± 0.00	5.02	**0.0001**
Worker size	0.07 ± 0.07	1.11	0.2803	0.12 ± 0.06	2.14	0.0444
Worker polymorphism	0.02 ± 0.07	0.28	0.7797	0.01 ± 0.04	0.29	0.7730
Diurnality	−0.10 ± 0.06	−1.48	0.1525	0.03 ± 0.01	2.06	0.0517
Dominance	−0.09 ± 0.07	−1.41	0.1719	0.04 ± 0.01	3.88	**0.0009**
Diet – seed-eating	0.61 ± 0.42	1.46	0.1598	0.10 ± 0.05	2.00	0.0587
Diet – insect-eating	0.00 ± 0.06	0.00	0.9971	0.05 ± 0.02	2.56	0.0182
Diet – liquid food-eating	−0.00 ± 0.06	−0.06	0.9543	0.06 ± 0.02	3.43	**0.0025**
Reproduction	0.01 ± 0.01	1.18	0.2501	0.01 ± 0.01	0.67	0.5097
Ratio queen/worker size	0.08 ± 0.05	1.53	0.1417	0.01 ± 0.03	0.29	0.7770
Colony foundation type	0.02 ± 0.05	0.48	0.6343	0.05 ± 0.07	0.78	0.4453
All together	−0.00 ± 0.00	0.29	0.7746	0.00 ± 0.00	3.66	**0.0015**

To understand the patterns of trait-composition changes we need to address the fire effects on biotic communities. On the one hand, fire destroys the nest and the entire colony of species that nest in vegetation (Arnan et al. 2006, Frizzo et al. 2012). In fact, the vegetation-nesting species are almost extinct in burned areas of the study area (Arnan et al. 2006), and a decrease in the traits associated to those species might be expected in burned areas, as seems to be the case in our study (see below). On the other hand, it is likely that most ground-nesting species were able to survive immediately after the fire because the increase in temperature is negligible at a few cm below ground surface (DeBano 2000). However, they have to cope with fire-induced environmental changes, in particular a much hotter environment, modified food resources availability and reduced habitat structural complexity (Castaño-Meneses and Palacios-Vargas 2003, Arnan et al. 2007a, Lázaro-González et al. 2013). Specifically, a drastic reduction in tree cover and a similar or even increased herbaceous and shrub cover characterized burned habitats of our study area (Supplementary material Appendix 1). A recent study has shown that traits of ants are clearly associated with the environment in which they occur (Wiescher et al. 2012) through environmental filtering.

Table 4. Summary of the Spearman rank correlations conducted to investigate the effects of dominant and rare species traits in overall community traits, and also to investigate similarity in trait composition between dominant and rare species. All the comparisons were conducted for each trait (either the average and the dissimilarity) and group of traits (functional diversity of social structure, resource exploitation, reproduction and overall traits). Numbers refer to the number of traits (or groups) where correlations were significant and with r > 0.7. The complete correlation results are given in Supplementary material Appendix 6.

Comparison	Trait average n traits/6 $p < 0.001$ and $r > 0.7$	Functional diversity n traits(or groups)/16 $p < 0.001$ and $r > 0.7$
Abundance data set		
All species vs dominants	**6**	**16**
All species vs rares	0	0
Dominants vs rares	0	0
Occurrence data set		
All species vs dominants	1	5
All species vs rares	**6**	**11**
Dominants vs rares	0	1

The colony size of ant colonies was higher in burned than in unburned areas (Fig. 2). The ecological advantages of large colony size in social insects include increased defense, homeostasis and work ability and greater ability to manipulate the surrounding environment (Bourke 1999). Consequently, the larger the ant colony, the better it can buffer disturbance effects, which might lead to a disappearance of the smallest ant colonies after fire. Moreover, we found larger ants in burned than in unburned areas when considering only occurrence data (Fig. 2). Several studies suggest a positive relationship between heat tolerance and body size in ants (Lighton and Feener 1989, Hood and Tschinkel 1990, Kaspari 1993), although this relationship has not recently been found at the community level (Wiescher et al. 2012). Effects on this trait are very relevant because the body size of an organism determines the quantity of resources consumed (Bihn et al. 2010). The occurrence of larger ants in burned habitats might also be determined by a simplification of habitat complexity, rather than an adaptation to a hotter environment. As the size-grain hypothesis predicts (Sarty et al. 2006, Gibb and Parr 2010), larger ant foragers have more advantages in lower- than in higher-complexity habitats (Farji-Brener et al. 2004). Worker polymorphism was also higher in burned areas (Fig. 2). Worker polymorphism has been related to the breadth of functional roles performed by colonies (Mertl and Traniello 2009, Arnan et al. 2011), and implies greater variability of responses to temperature, which increase the overall period of external activity, and enhances colony success (Cerdá and Retana 1997). Large workers can be active at higher temperatures and perform longer trips than small workers because of their longer legs, which allow them to stilt above the hot substrate, or their greater running speed (Heinrich 1993). Looking at the specific patterns, we observed an increase in abundance and/or occurrence in burned areas of some species associated with the highest values of these three traits. These patterns are mostly driven by the large populated colonies of *Lasius niger* (the most abundant species in this study), *Tetramorium semilaeve* and *Tapinoma nigerrimum*; the highly polymorphic species of *Messor* and *Cataglyphis* and *Pheidole pallidula*, as well as several large-sized and polymorphic species of *Camponotus*. However, at the same time, we also observed a decrease in the abundance and/or the occurrence of species with the lowest values of these traits. Interestingly, most of these species (mainly *Temnothorax* spp.) nest in the vegetation (with the exception of *Solenopsis latro*). The combination of these factors suggests that the set of functional responses we report here is related to direct mortality by fire as well as to the indirect fire-induced modifications in environmental conditions that are relevant to ants. Interestingly, the presence of large ants with larger colonies in burned than in unburned areas indicates that post-fire scenarios are favor ant productivity. The ratio between queen and worker size of most abundant species was also higher in burned areas (Fig. 2). One explanation here may lie in the relationship between high queen/worker ratio and independent colony founding (Amor et al. 2011). This reproduction strategy provides dispersal advantages at long distances in relation to dependent colony-founding strategies (Amor et al. 2011), which could indicate that species with this kind of dispersal strategy are more likely to colonize burned areas. The increase could be a reflection of the strategy of the species that newly colonized the burned area. All species that increased their abundance in the burned areas displayed high values of this index, *L. niger*, *Camponotus piceus*, *P. pallidula*, *Plagiolepis pygmaea* and *Formica subrufa* being the species with the highest values. However, if that were so, some effect should have been detected in the colony foundation type, and this was not the case. One continuous variable is always more precise than a qualitative variable, but the relationship between these two functional traits and the mechanism by which fire affects them still remain unclear.

We found that trait dissimilarity of behavioral dominance was higher in burned areas (Fig. 2). This pattern is driven by an increase in the proportion of behaviorally dominant species (Supplementary material Appendix 3), following the global pattern of behavioral dominance in relation to environmental stress and disturbance (Andersen 1995). However, this pattern was unexpected in a Mediterranean area such as ours. As a rule in the Mediterranean basin, subordinate ant species prefer to inhabit open areas with particular environmental conditions, mainly high temperatures at midday and low competition from behaviorally dominant species, which are more abundant in forests where temperature is lower (Cerdá et al. 1997, 1998). One explanation may be found in some deviations from this general rule, because Mediterranean behaviorally dominant and subordinate species can be classified into different subgroups in relation to different functional traits that allow them to cope with particular conditions across environmental gradients (Arnan et al. 2012). One subgroup of subordinate species is composed by species with low heat tolerance. Again, they are mainly species of the genus *Temnothorax* that nest in the vegetation. For this reason, behavioral dominance might be higher in burned areas due to a drastic reduction in these species by direct fire-destruction of their colonies. Accordingly, we observed that all species that were removed from unburned areas were subordinates (mainly *Temnothorax* spp.), while the species that colonized the burned areas were classified as dominants and subordinates (mainly *Camponotus* spp.). This pattern therefore seems to be driven by a reduction of subordinates, rather than an increase in behavioral dominants in burned areas. At the same time, trait dissimilarity in liquid food consumption was also higher in burned areas. This pattern comes from an increase in the proportion of liquid food in diet, which suggests a remarkable change in trophic positions. Fire is known to increase the presence of plant species with entomophilous flowers (Potts et al. 2003) and, in relation to that, we observed an increase in species (such as several species of *Camponotus* plus *Tapinoma nigerrimum* and *Lasius niger*) with a high degree of this food in their diet rather than a decrease in species with low liquid food preferences in burned areas.

It is worth noting some high correlations among these functional traits at the community level (Supplementary material Appendix 4, 5), which call into question whether some of these functional changes are directly driven by fire, but they are also the reflection of a covariation between non-independent traits. In our case it seems to be a combination of both effects. First, there might exist a syndrome of traits related to vegetation-nesting ability at specific level, such as small colonies, small worker size and low polymorphism, which decline due to the direct effects of fire. And second, such correlations at community level might also be explained by different traits that follow parallel trends in response to fire, because the increase in the trait values in the burned areas is also driven by the arrival and/or the increase in abundance of species with the highest values, which are not always correlated with one another.

Interestingly, different patterns of trait composition changes arise from the comparison of results from abundance and occurrence data. The functional response to fire in trait averages is quite similar, with little variation when considering species abundance or species occurrence (Fig. 2). Consequently, the response of ant communities to fire is driven at the same time by replacement of species with different traits and by changes in the relative abundance-dominance of species (de Bello et al. 2007). However, in the case of trait dissimilarity, the response to fire is much more marked when considering occurrence rather than abundance data (Fig. 2). Since species richness is similar between burned and unburned sites of the study area (Arnan et al. 2006), this implies, on the one hand, that the functional fire-induced change in ant communities is based on a replacement of species with different traits. Moreover, our results highlight that such replacement is mainly driven by rare species, which possess different trait composition than dominants. On the other hand, the traits of the most abundant-dominant species remain relatively stable. Thus, we suggest that fire promotes higher functional diversity driven primarily by rare species that are functionally unique. Although it is thought that ecosystem functioning is largely controlled in the short term by dominant species (Grime

1998), rare species often possess unique combinations of functional traits (Bihn et al. 2010) and can make significant contributions to ecosystem functioning (Lyons et al. 2005). Then, we found relevant changes in the trait composition of western Mediterranean ant communities, which may affect function (Díaz et al. 2007). Further research is needed to elucidate how these patterns can be generalized to other Mediterranean regions or other biogeographic areas.

The increased functional diversity due to fire bore a clear relationship to resource exploitation-related traits (Fig. 2), as we found significant effects on trait dissimilarity of single traits and their combination when taking into account occurrence data. Indeed, overall functional diversity was highly correlated to trait dissimilarity of some resource exploitation traits and their combination (Supplementary material Appendix 5). Functional diversity is an indicator of how the species share the niche space available (de Bello et al. 2006). A higher diversity of foraging strategies in burned areas might be related to a greater volume and occupation of niche space in burned areas than in unburned areas. This might be mediated by the creation of new niches by fire (e.g. higher thermal contrasts) or by higher niche partitioning in the same volume of niche space through higher competitive pressures due to an eventual more relative abundance of behaviorally dominant species in burned areas. Alternatively, this pattern might be related to the mid-time scale of this study, i.e. eight years after fire, where at intermediate time-scales after the disturbance a higher number of species with different strategies might likely co-occur, similar to that predicted by the intermediate disturbance hypothesis with species richness. However, as far as we know there are no studies testing this relationship.

Our results contrast with other works that find no or very little significant functional responses to fire in other Hymenopterans in Mediterranean regions (Moretti et al. 2009 for bee species, Mateos et al. 2011 for different Hymenoptera groups), displaying a high functional redundancy. The relevant functional changes that we have found suggest a low functional redundancy in response to environmental change (Petchey et al. 2007, Moretti et al. 2009) due to fire in our study area, which clearly contradicts the expectations of high stability in response to perturbation (i.e. high resistance and resilience to disturbance) under a severe evolutionary selection by fire in Mediterranean areas (Moretti et al. 2009). However, the inherent biology of the group they analyzed (bees) is clearly different to ants. In spite of the low functional redundancy in response to fire, in our study area functional diversity increases rather than decreases in the post-fire scenario. Since the reported increase in functional diversity is not directly related to an increase in species richness (Arnan et al. 2006), a decrease in functional redundancy and, consequently, lower ecosystem stability in the post-fire scenario (Díaz and Cabido 2001) might be predicted. Indeed, in our study area the increase in functional diversity arises when considering occurrence data, and is mostly driven by rare species. These species are especially prone to extinction (Gaston 1994), and later disturbances could lead to rapid loss of ecosystem functioning. It is thus of great interest to see how functional changes affect communities' resilience to other disturbances, and especially to the predicted climate change.

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Supplementary material (Appendix ECOG-00155 at <www.oikosoffice.lu.se/appendix>. Appendix 1–6.