

# Short-term ecological and behavioural responses of Mediterranean ant species *Aphaenogaster gibbosa* (Latr. 1798) to wildfire

ALBA LÁZARO-GONZÁLEZ,<sup>1</sup> XAVIER ARNAN,<sup>2,3</sup> RAPHAEL BOULAY,<sup>4,5</sup> XIM CERDÁ<sup>4</sup> and ANSELM RODRIGO<sup>1,2</sup> <sup>1</sup>Univ Autònoma Barcelona, Cerdanyola del Vallès, Spain, <sup>2</sup>CREAF, Cerdanyola del Vallès, Spain, <sup>3</sup>Faculty of Biology, TU Darmstadt, Darmstadt, Germany, <sup>4</sup>Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas (CSIC), Seville, Spain and <sup>5</sup>Departamento de Zoología, Universidad de Granada, Granada, Spain

**Abstract.** 1. Fire greatly affects plant and animal biodiversity. There is an extensive body of literature on the effects of fire on insect communities, in which a large variability of responses has been observed. Very few studies, however, have addressed functional responses at the species level, information that would greatly enhance our understanding of the impact of fire at higher organisational levels.

2. The aim of this study is to analyse the short-term ecological and behavioural responses of the Mediterranean ant *Aphaenogaster gibbosa* to fire-induced environmental changes. We compared aspects of the abiotic and biotic environment relevant to this species, as well as differences in colony foraging behaviour, on unburnt and burnt plots in a Mediterranean area that was affected by a wildfire.

3. Our results showed that fire modified plant cover around nests and daily cycles of soil temperature close to the nest. Although there were no significant differences in food quantity, food quality (particularly seed composition) was different between unburnt and burnt plots.

4. In accordance with these environmental changes, we found significant differences in the daily activity rhythms and diet composition of *A. gibbosa* between unburnt and burnt plots. Overall, these differences did not result in significant changes in overall foraging activity and efficiency, allowing ant colonies to maintain the same food intake regardless of the habitat they occupied.

5. We conclude that *A. gibbosa* uses behavioural plasticity to modify its foraging strategy in recently burnt environments and thus survive post-fire conditions.

**Key words.** Ants, behavioural plasticity, colony spatial patterns, daily activity rhythms, diet, fire, foraging, omnivory, seasonality, temperature.

## Introduction

Fire is an important natural disturbance in many ecosystems that affects community structure and composition

Correspondence: Xavier Arnan, Facultat de Biociències, CREAF (Centre de Recerca Ecològica i Aplicacions Forestals), Universitat Autònoma de Barcelona, E-08193 Bellaterra, Catalunya, Spain and Faculty of Biology, TU Darmstadt, Schnittspahnstrasse 3, D-64287 Darmstadt, Germany. E-mail: x.arnan@creaf.uab.es

(Swengel, 2001; Andersen *et al.*, 2005), particularly in the Mediterranean biotopes (Gill *et al.*, 1981; Whelan, 1995). Fire also causes important modifications in environmental conditions and resource availability both in the short- and long term (Noble & Gill, 1981). These significant modifications may change the structure and composition of both plant and animal communities by altering the quality and quantity of species interactions (Gill *et al.*, 1981). Although responses to fire by animal communities are taxon dependent, at the regional level fires usually benefit species preferring open habitats to the detriment of forest

specialists (Paquin & Coderre, 1997; Brotons *et al.*, 2005; Moretti *et al.*, 2006; Rodrigo *et al.*, 2008; Pastro *et al.*, 2011; Schowalter, 2012).

Ants are crucial components of most terrestrial ecosystems, contributing significantly to faunal biomass and the modification in the abiotic and biotic properties of their environment (Hölldobler & Wilson, 1990; Folgarait, 1998; Retana *et al.*, 2004; Arnan *et al.*, 2011). Fire has been shown to increase (Andersen, 1991a; Jackson & Fox, 1996) or decrease (York, 1994) ant abundance, depending on the habitat (Folgarait, 1998). Similarly, studies have found that fire may increase (Andersen *et al.*, 2006, 2009), decrease (Farji-Brener *et al.*, 2002), or have no effect (Parr *et al.*, 2004; Arnan *et al.*, 2006) on ant species richness depending on biotic and abiotic conditions, such as climate and vegetation type (Arnan *et al.*, 2006; Barrow *et al.*, 2007). Furthermore, even in cases in which species richness does not differ between adjacent burnt and unburnt areas, ant community composition can be very different (Castaño-Meneses & Palacios-Vargas, 2003; Arnan *et al.*, 2006). Consequently, the responses of ants to fire can be species specific (Arnan *et al.*, 2006; Rodrigo & Retana, 2006; Frizzo *et al.*, 2012). In spite of this broad literature dealing with the consequences of fire for ant communities, very few studies have investigated the functional response at the species level (but see McCoy & Kaiser, 1990; Zimmer & Parmenter, 1998). This information, however, is necessary to better understand the impact of fire at higher organisational levels.

Although fire directly causes the death of ants that nest in the vegetation, the increase in temperature is negligible at a few centimetres below the ground surface, allowing most ground-dwelling species to survive (Arnan *et al.*, 2006; Frizzo *et al.*, 2012). Fire-induced modifications in vegetative physiognomy and composition, however, may have important negative or positive indirect effects on ground-dwelling ants in the mid- to long term (Arnan *et al.*, 2006; Rodrigo & Retana, 2006). For example, in hot environments, the suppression of vegetative cover may increase ground temperature and limit habitat use by non-thermophilic ants (Andersen, 1990, 1991b; Folkerts *et al.*, 1993; Boulay *et al.*, 2009). In addition, the modification in plant composition may directly or indirectly affect the availability of resources such as seeds, nectar, aphid honeydew, and the corpses of herbivorous insects (Rodrigo & Retana, 2006; Arnan *et al.*, 2007). Nevertheless, the indirect effect of fire on ground-dwelling ants is expected to vary between species depending on their capacity to adjust their behaviour to the new conditions. In particular, during the post-fire successional stage, omnivorous species may be able to shift their diet towards the most abundant resources until pre-fire conditions are restored.

An animal's ability to adjust its foraging behaviour is thought to condition its tolerance to environmental changes (Gordon, 1991). Thus, the analysis of foraging activity would reveal the basic mechanisms used by ant species to confront the new conditions created by fire. For

example, fire-induced modifications in microclimatic conditions may change both the population size of workers that forage and their foraging efficiency. By adjusting their daily activity rhythm, ants could face microclimatic adversity in burnt areas. In addition, fire-induced modifications in food quantity and quality could cause major changes in the diet of these species, and how they gather food resources. It has been recognised that resource characteristics may also affect the foraging behaviour of ant colonies (Traniello, 1989; Gordon, 1991; Sundstrom, 1993). Fire-induced changes could not only affect the spatial distribution and abundance of resources themselves but also alter microclimatic conditions and eliminate obstacles to locomotion that could also influence the distance ants travel to collect food (Bernadou & Fourcassié, 2008; Clay *et al.*, 2010).

*Aphaenogaster gibbosa* (Latr, 1978) is a widely distributed Mediterranean ant species and, like many other Mediterranean ant species, is omnivorous (Bernard, 1968). Previous studies have suggested that forager abundance in this species does not seem to be affected by fire (Arnan *et al.*, 2006; Rodrigo & Retana, 2006). They only examined the effect of fire on the abundance of ground-foraging workers captured with pitfall traps, however. In contrast, this study aims to analyse the short-term ecological and behavioural responses of *A. gibbosa* to fire-induced environmental changes. We first describe the fire-induced modifications in the abiotic (soil and ground temperatures and plant cover near nests) and biotic (resource availability) environment. We then determine whether the abundance (density and spatial patterns) and foraging behaviour (daily and seasonal activity, foraging distances, foraging efficiency, and diet) of *A. gibbosa* colonies are affected by the fire-induced changes.

## Materials and methods

### Study system

This study was carried out during the spring of 2011 in Salo, Barcelona (North-eastern Spain, 1°38'E, 41°51'N, 519-642 m above sea level). The local climate is Mediterranean, with a mean annual temperature of 12.4 °C and a mean annual rainfall of 626.4 mm. In June 2009, a canopy wildfire burnt an area of 194 ha that included a pine forest (74% of the area; dominated by *Pinus nigra* and *P. halepensis*), croplands (24%), and shrublands (2%) (Centre de Recerca Ecològica i Aplicacions Forestals (CREAF), 2010). Two years after the fire, the same area had been taken over by shrublands, which were dominated by sprouts of *Quercus coccifera*, *Arbutus unedo*, and *Q. ilex*, and grasslands, which were dominated by *Brachypodium phoenicoides* and *B. retusum*. We conducted our study in areas previously dominated by *P. nigra* forests that were affected by canopy fires, where pine regeneration was almost nil.

*Aphaenogaster gibbosa* is a common ant species that is distributed across the western Mediterranean basin, principally in areas with calcareous soils (Bernard, 1968). At our study site, it is one of the most common species, along with *Pheidole pallidula*, *Crematogaster scutellaris*, *Formica gagates*, *F. gerardi*, and *Myrmica spinosior* (X. Arnan, R. Boulay, X. Cerdá, A. Rodrigo, unpubl. data). *A. gibbosa* is, however, subordinate and frequently loses food resources to other ant species (Arnan *et al.*, 2012). Colonies are monodomous and monogynous and contain  $405 \pm 34$  workers (mean  $\pm$  SE,  $n = 42$ ; S. Caut, M.J. Jowers, X. Arnan, J. Pearce-Duvel, A. Rodrigo, X. Cerdá, & R. Boulay, unpubl. data). It has been described as an omnivorous species (Bernard, 1968). Although workers mostly forage solitarily, they can occasionally recruit small groups of nestmates to retrieve large prey items.

### Experimental design

The study was conducted in three pairs of  $30 \times 30$  m plots. In each pair, one plot was located in the burnt area (hereafter, B) and the other was located in the surrounding unburnt area (hereafter, UB). As B and UB plots of each pair had similar aspects and slopes, the two plots of each pair were assumed to be more similar in pre-fire composition to each other than to plots in other pairs. Plots within pairs were separated by approximately 300 m, whereas different pairs of plots were separated by approximately 1200 m. In late March 2011, four focal *A. gibbosa* nests were selected in each plot. They were separated by at least 7 m to avoid interference between them. We thus studied a total of 24 *A. gibbosa* nests: 12 in B and 12 in UB areas. We quantified each colony's foraging activity, as well as the abiotic and biotic conditions it experienced during the period of study.

### Nest density and spatial distribution

First, we wanted to ensure that fire did not have a detrimental effect on ant colony density and spatial distribution. To this end, all nests present in each plot were mapped in mid-May 2011, when the activity of most ant species was the highest (Cros *et al.*, 1997). An  $8 \times 8$  grid of 64 baits separated by 3 m was set up in each plot. Baits consisted of cookie crumbs attractive to *A. gibbosa* workers. On each plot, baiting took place once in the morning and once in the afternoon on two different days. As the number of new nests discovered over time approached an asymptote, our sampling appears to have been relatively exhaustive. From these maps, we calculated nest density and mean nearest-neighbour nest distance for each plot. The spatial distribution of *A. gibbosa* colonies in each plot was analysed using the R aggregation index (Clark & Evans, 1954), and its significance was tested using a Z-test. This index was not applied to one UB plot in which nest density was too low (see results).

### Abiotic conditions

**Temperature.** A data logger (HOBO Pro v2) was placed directly on the ground in the centre of each plot to record ground temperature (plot temperature) every 30 min from early April to early-June, which covered the period during which foraging activity was studied (see below). Soil temperature was also recorded near the nest entrance (nest temperature) with an infrared temperature gun (Raytek MT4) every hour from 8 a.m. to 8 p.m. on the days on which *A. gibbosa* activity was measured ( $n = 5$  observation days, see below). For each observation day, we then calculated the daily mean temperature and the coefficient of variation (CV, which is standard deviation/mean of hourly temperatures) in temperature at both the plot and nest level.

General linear mixed models (GLMMs) were used to test the effects of fire, observation day, and their interaction (fixed factors) on the four temperature variables (mean and CV of plot and nest temperatures). In the GLMMs examining plot temperature, plot and plot pair were included as random factors; in the GLMMs examining nest temperature, the random factors were nest, plot, and plot pair. Hourly nest temperatures were fitted to separate general non-linear mixed models for each observation day. Fire status (B/UB), time of day, and their interaction were treated as fixed factors, whereas nest, plot, and plot pair were included as random factors. The response variable was not linear over time, therefore (Time of day)<sup>2</sup> and its interaction with fire were added to the model as fixed factors. This quadratic term indicates which way the curve is bending.

**Cover around nests.** A  $5 \times 5$  m plot was delimited around each focal nest, and three  $1 \times 5$  m bands were sampled within each square. Each band was divided into eighty  $0.25 \times 0.25$  m cells in which cover was categorised as rock, bare soil, litter, wood debris, herb, or shrub. From the three  $1 \times 5$  m bands, we calculated the percentage of cover provided by each category to the total cover around the nest. Plots of the same pair were sampled on consecutive days.

Differences in different categories of cover around the nests between B and UB plots were analysed using a GLMM. Fire status, cover category, and their interaction were treated as fixed factors, and plot pair and plot were included as random factors. The percentage cover was square-root transformed to meet the assumption of homoscedasticity. As the interaction was significant (see results), we carried out multiple comparison tests to clarify significant differences among the different combinations of cover category and fire status. Note that the sum of the cover of each category is 100%; to avoid data dependence, we did not include the categories litter (only found in UB plots) and rock cover (the less common cover type) in the analysis.

### Biotic conditions

**Availability of food resources – arthropods and plant material.** We used pitfall and yellow pan traps to sample

arthropod prey items available as food sources for each nest. Pitfall traps were 7-cm diameter, 9.5-cm deep plastic vials, whereas yellow pan traps consisted of plastic plates 4.5-cm high and 15-cm diameter. Both types of traps were filled with a mixture of water, soap, and salt. We placed two yellow pan traps 1 m from the nest, one to the right side and one to the left side. Four pitfall traps were located 2.5 m from the nest, forming a square around it. The distances at which we placed the traps represented a compromise between the maximum foraging distance of this species (see Results) and the adequate distance needed between traps to ensure their independence. Both pitfall and yellow pan traps were used to sample arthropods (ground-dwelling and flying arthropods, respectively) that could potentially be collected dead or alive by *A. gibbosa*. Arthropod sampling was conducted once a month in April, May, and June. During each sampling event, pitfall and yellow pan traps were active for 72 and 24 h, respectively. All arthropods were preserved in 70% ethanol, dried at 80 °C for 48 h, and weighed to the nearest 0.01 mg to estimate the biomass (g per trap\*day) available to each ant colony. Data from the three different sampling events were pooled to be compared with the samples of *A. gibbosa*'s diet (see below), for which only a single value could be estimated for the entire season due to the small number of items collected during sampling.

Differences in available arthropod biomass (ground dwelling and flying) between UB and B plots were analysed using GLMMs, where fire status was included as a fixed factor and plot pair and plot as random factors. The biomass of ground-dwelling arthropods was log-transformed. Ground-dwelling and flying arthropods were analysed separately due to the different traps used to sample each group.

To analyse plant resource availability for each ant colony, we used the same three bands (15 m<sup>2</sup>) used to characterise cover around the nests. We measured the seed production of all plant species in the forest understory and the number of petals of *Argyrobium zanonii*, *Fumana ericoides*, *Helianthemum strictum*, and *Rosmarinus officinalis* on a monthly basis (April, May, and June). Preliminary observations suggested that these petals are often collected by *A. gibbosa* in the study area. This kind of food resource is commonly used by *Aphaenogaster* species to feed workers and larvae (Cerdá *et al.*, 1988, 1996). To measure seed production, we counted the number of mature fruit for each plant species. We only considered mature fruit that had already released seeds or were about to do so, assuming that these seeds were already, or soon would be, available to ants. We also collected between 30 and 200 fruits from each plant species outside the plot and estimated the mean number of seeds per fruit. We then calculated the total number of seeds produced per plant species and per unit area around the nests. Seed samples were dried at 80 °C for 48 h and then weighed to an accuracy of 0.01 mg. We then calculated the seed and petal density (n m<sup>-2</sup>) and seed biomass (g m<sup>-2</sup>) for each plant species around each nest for the entire sampling period.

Differences in total seed biomass and seed number between fire status categories (fixed factor) were analysed using two different GLMMs, where plot pair and plot were included as random factors. In addition, significant differences in the assemblage composition of seeds available to *A. gibbosa* between B and UB areas were determined with multivariate analysis using the program Primer 5.1.2 (Clarke & Gorley, 2001). Seed biomass per nest was square-root transformed to reduce the weighting effect of abundant species, but preserve relative biomass information (Clarke, 1993); it was also used to generate Bray–Curtis similarity measures. First, nests were ordered using non-metric multidimensional scaling based on the Bray–Curtis similarity matrix. Then, analysis of similarities (ANOSIM) was used to establish significant differences in the assemblage composition of seed biomass related to fire status (B and UB). Seed species that had a relative seed biomass of <0.5% were excluded from the analysis. Finally, similarity percentages (SIMPER) were used to identify the seeds that most contributed to differences in assemblage composition. To compare the relative availability of seeds and petals between fire status categories, we used a chi-squared test. We examined the total number of seeds and petals available (rows) between UB and B plots (columns); data were pooled across nests and plots.

#### *Foraging activity, foraging distance, and diet of A. gibbosa*

*Daily and seasonal activity rhythms and foraging efficiency.* The foraging activity (FA) and efficiency (FE) of each *A. gibbosa* focal colony were measured every 15 days between mid-April and early-June ( $n = 5$  observation days). To assess hourly FA, all loaded and unloaded workers entering the nest were counted during 10-min sessions that took place every hour from 8 a.m. to 8 p.m.; worker numbers per hour were extrapolated from these counts. Daily FA was the sum of the hourly FA for a given nest. FE was calculated as the proportion of incoming workers that carried a food item.

The effects of fire status, observation day, and their interaction on daily FA and FE were tested by fitting general linear mixed models (GLMMs). Fire status, observation day, and their interaction were included as fixed factors, and plot pair, plot, and nest were included as random factors. Daily FA and FE were square-root and arcsin square-root transformed, respectively, to meet the assumption of homoscedasticity. Daily activity rhythms were fitted to generalised non-linear mixed models with error modelled as a binomial distribution; a different model was fit for each observation day. As there were many inactive colonies, i.e. colonies for which there were hours without any incoming workers, we treated FA as a binary variable (1, active; 0, no active). Fire status, hour of the day, and their interaction were treated as fixed factors and plot pair, plot, and nest as random factors. As the activity of *A. gibbosa* throughout the day was not

linear (A. Lázaro, Pers. Obs.; see Appendix S1), (hour of the day)<sup>2</sup> and its interaction with fire were also added to the model.

*Foraging distances.* Foraging distance was estimated during nest mapping as the average distance between a given nest and all the baits visited by workers of this nest. A GLMM was used to test the effect of fire status (fixed factor) on square-root transformed foraging distances, with plot pair and plot included as random factors.

*Diet.* The abundance and composition of *A. gibbosa*'s diet was sampled by collecting the food items carried by incoming workers at the nest entrance. We conducted sampling three different times (in April, May, and June) per plot over the study period. The four nests of a given plot were sampled in a single day, from 8 a.m. to 8 p.m. We sampled the nests that looked like they had greater activity first. Collected items were kept in vials and classified as arthropod, plant (seeds, petals, or plant debris), or other. All collected samples were dried at 80 °C for 48 h and weighed to the nearest 0.01 mg. The samples for each nest were combined across months, and the relative proportions of arthropod and plant items (dry weight and abundance) were then calculated.

Differences between UB and B plots in the relative proportion of animal items (both abundance and dry weight) in the diet of *A. gibbosa* were analysed using GLMMs, where fire status was included as a fixed factor and plot pair and plot as random factors. Both dependent variables were square-root transformed. We conducted a chi-squared test to analyse differences between UB and B plots in the relative abundance of petals, seeds, and plant debris that composed *A. gibbosa*'s diet. We compared the total frequency of each of these categories (rows) on UB and B plots (columns); data were pooled across nests and plots.

All statistical analyses were conducted using the R software system, version 2.10.1 (R Development Core Team, 2010). Generalised linear and non-linear mixed models were conducted using the function *lmer* of the *lme4* package, whereas general linear and non-linear mixed models were carried out using the function *lme* of the *nlme* package. We have included the ANOVA tables for these analyses (with the exception of the generalised models) in the

results section. We used the Bonferroni correction to control for our multiple comparisons.

## Results

### *Nest density and spatial distribution*

Nest density was similar between B and UB plots and ranged from 0.06 to 0.10 nests m<sup>-2</sup>, except on one UB plot where nest density was 0.009 nests m<sup>-2</sup>. The mean distance between neighbouring nests was 2.29 ± 0.09 m (plot with low density was excluded). Overall, nests were regularly distributed ( $R = 1.3$ ,  $Z = 2.7$ ,  $P = 0.01$  and  $R = 1.3$ ,  $Z = 4.1$ ,  $P < 0.001$  for the two UB plots analysed; and  $R = 1.2$ ,  $Z = 2.2$ ,  $P = 0.03$ ;  $R = 1.5$ ,  $Z = 6.5$ ,  $P < 0.001$  for the B plots); however, on one B plot, nest distribution was not significantly different from the random distribution ( $R = 1.1$ ,  $Z = 1.1$ ,  $P = 0.13$ ).

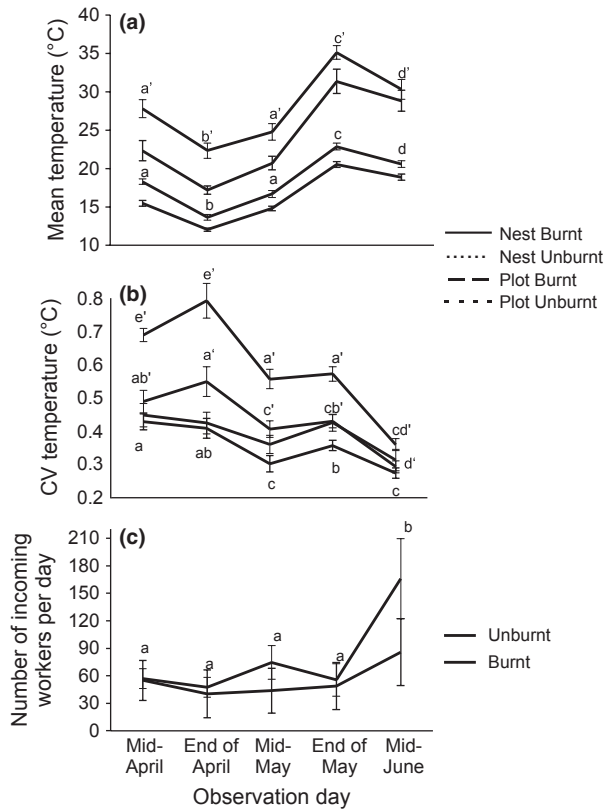
### *Abiotic conditions, foraging activity, and foraging distance*

Mean plot temperature was significantly different over the period of observation (Table 1), with the lowest temperatures occurring in late April and the highest in late-May and mid-June (Fig. 1a). Neither fire status nor its interaction with observation day had a significant effect on plot temperature (Table 1). This interaction, however, was significant for the CV of plot temperature (Table 1). Daily temperature variation was higher on B than on UB plots, but these differences decreased over time; furthermore, temperature fluctuation was also greater in mid-April than in mid-June on both UB and B plots (Fig. 1b). The mean and CV of nest temperatures showed significant differences across sampling days but not between B and UB plots, and the interaction between fire status and observation day was not significant (Table 1). Mean nest temperatures were lowest in April and mid-May and highest in late-May and mid-June (Fig. 1a). The greatest temperature fluctuation was recorded in mid-April and the least amount of change was seen at the end of May and in mid-June (Fig. 1b).

Daily mean FA was more than two-fold higher in mid-June than at any other time (GLMM,  $F_{4,88} = 6.3$ ,  $P = 0.0002$ ; Fig. 1c). Daily mean FA, however, did not

**Table 1.** The effect of fire status (fire; burnt and unburnt), observation day (day), and their interaction on plot and nest temperatures. *F*-values, significance (*P*), and degrees of freedom (d.f.) come from the GLMM ANOVA tables.

Factors	Plot temperature						Nest temperature					
	Mean			Coefficient of variation			Mean			Coefficient of variation		
	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
Fire	1, 2	10.6	0.08	1, 2	8.6	0.10	1, 2	6.2	0.13	1, 2	1.9	0.29
Day	4, 16	174.6	<0.0001	4, 16	83.4	<0.0001	4, 106	55.3	<0.0001	4, 88	16.5	<0.0001
Fire*Day	4, 16	0.9	0.50	4, 16	4.6	0.01	4, 106	1.6	0.19	4, 88	0.6	0.63

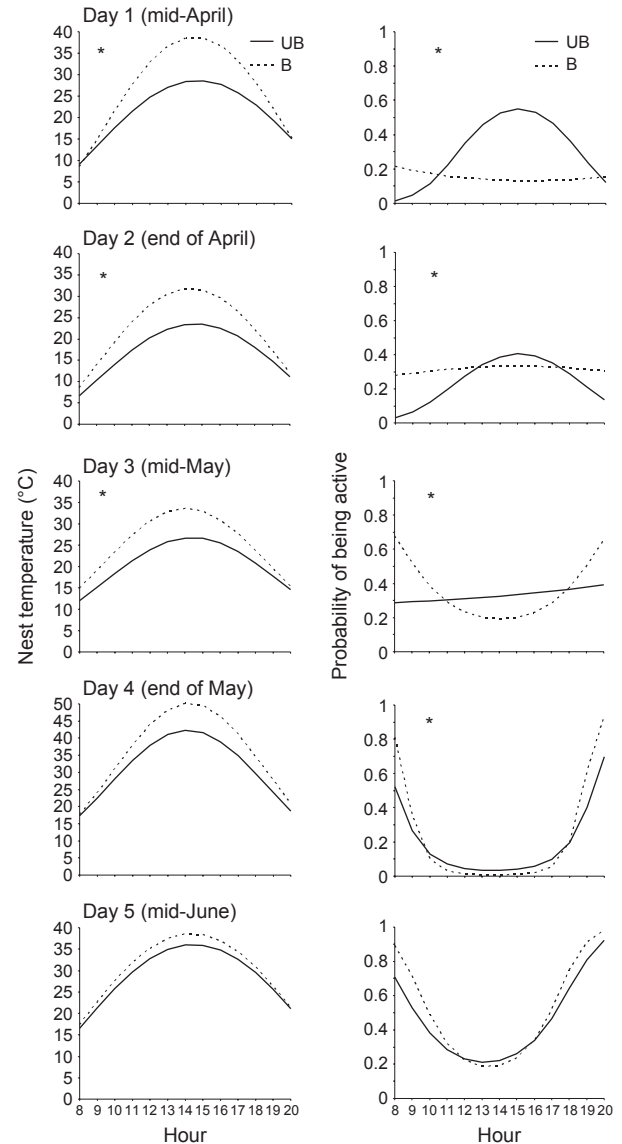


**Fig. 1.** (a) Mean ( $\pm$ SE) and (b) coefficient of variation ( $\pm$ SE) in plot and nest temperatures; (c) mean foraging activity (number of workers entering the nest per day) ( $\pm$ SE) for the different observation days in burnt and unburnt areas. Different letters indicate significant differences based on multiple comparison tests to which the Bonferroni correction was applied.

differ significantly between B and UB plots ( $F_{1,2} = 0.5$ ,  $P = 0.54$ ), and the interaction between fire status and observation day was not significant ( $F_{4,88} = 0.9$ ,  $P = 0.50$ ). Daily mean FE per colony did not differ between UB and B plots (GLMM,  $F_{1,2} = 1.9$ ,  $P = 0.30$ ) or among observation days ( $F_{4,74} = 1.5$ ,  $P = 0.21$ ); the fire status-observation day interaction was also not significant ( $F_{4,74} = 1.1$ ,  $P = 0.39$ ).

The daily cycles of nest temperature displayed a consistent pattern for all observation days (Fig. 2; Appendix S1). Temperature was higher in the middle of the day and lower in both the morning and afternoon (Fig. 2). There was an effect of fire status on nest temperature at the end of April; fire status also interacted with the hour of the day in April and with the (hour of the day)<sup>2</sup> in mid-May, but not at the end of May and in mid-June (Table 2). For all the interactions present, nest temperature was globally higher in B than in UB plots in the course of the day, and this pattern was specially accentuated in the middle of the day (Fig. 2).

The daily activity rhythms showed a quadratic relationship on all observation days, except in mid-May



**Fig. 2.** Nest temperature (left) and daily rhythms of ant activity (right) in B and UB plots for the five observation days. Values correspond to the marginal values fitted from the respective models. Asterisks mean there was a significant effect of fire status (B, UB) or that it interacted with time of day (see also Tables 1 and 3).

(Table 3): the relationship was mainly hump shaped in mid-April and at the end of April and U-shaped at the end of May and in mid-June (Fig. 2; Appendix S1). The shape of the function was also modulated by fire (Fig. 2), as evidenced by the significant interaction between fire and time of day and fire and (time of day)<sup>2</sup> for all observation days except the one in mid-June (Table 3). As a rule, the probability of being active was higher in UB than in B plots in the middle of the day, and this pattern was reversed in the early and late hours of the day (Fig. 2).

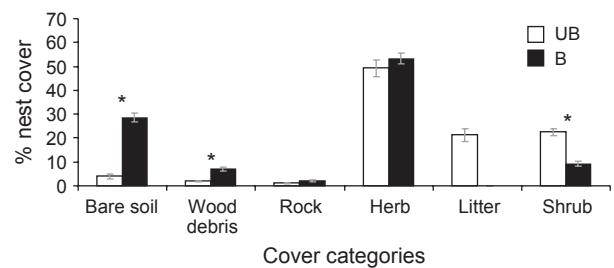
**Table 2.** Effect of fire status (fire; burnt vs. unburnt plots) and time of day (h) effects on nest temperature for each observation day. *F*-values, significance (*P*), and degrees of freedom (d.f.) come from the ANOVA tables of the fitted general non-linear mixed models. Note that Time<sup>2</sup> refers to the model's quadratic term.

Factor	d.f.	Day 1 (mid-April)		Day 2 (end of April)		Day 3 (mid-May)		Day 4 (end of May)		Day 5 (mid-June)	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Fire	1, 2	12.6	0.07	24.8	0.0380	6.0	0.13	2.0	0.29	0.5	0.54
Time	1, 284	68.9	<0.0001	37.3	<0.0001	8.7	0.0034	7.6	0.0062	24.5	<0.0001
Time <sup>2</sup>	1, 284	446.0	<0.0001	513.9	<0.0001	539.6	<0.0001	538.6	<0.0001	379.9	<0.0001
Fire*Time	1, 284	17.4	<0.0001	7.9	0.0053	1.6	0.21	2.1	0.15	0.6	0.43
Fire*Time <sup>2</sup>	1, 284	0.0	0.96	2.2	0.14	2.3	0.0129	0.7	0.42	0.3	0.61

**Table 3.** Effect of fire status (fire), time of day (time), and their interaction on *Aphaenogaster gibbosa* foraging activity. Summary statistics for the generalised non-linear mixed models with a binomial distribution were used to fit data for each observation day. Note that Time<sup>2</sup> refers to the model's quadratic term.

	Parameter	SE	Z	<i>P</i>
Day 1 (mid-April)				
Fire	20.4	5.5	3.7	0.0002
Time	2.7	0.6	4.3	<0.0001
Time <sup>2</sup>	-0.1	0.0	-4.2	<0.0001
Fire*Time	-3.0	0.8	-3.8	0.0002
Fire*Time <sup>2</sup>	0.1	0.0	3.6	0.0003
Day 2 (end of April)				
Fire	12.4	4.9	2.5	0.0121
Time	1.8	0.6	3.3	0.0011
Time <sup>2</sup>	-0.1	0.0	-3.2	0.0015
Fire*Time	-1.7	0.7	-2.3	0.0176
Fire*Time <sup>2</sup>	0.1	0.0	2.3	0.0234
Day 3 (mid-May)				
Fire	11.2	4.0	2.8	0.0047
Time	-0.0	0.4	-0.0	0.99
Time <sup>2</sup>	0.0	0.0	0.1	0.92
Fire*Time	-1.7	0.6	-2.8	0.0052
Fire*Time <sup>2</sup>	0.1	0.0	2.7	0.0061
Day 4 (end of May)				
Fire	15.2	6.6	2.3	0.0202
Time	-2.9	0.6	-5.0	<0.0001
Time <sup>2</sup>	0.1	0.0	5.0	<0.0001
Fire*Time	-2.4	1.0	-2.3	0.0189
Fire*Time <sup>2</sup>	0.1	0.0	2.4	0.0178
Day 5 (mid-June)				
Fire	7.8	5.0	1.6	0.18
Time	-2.2	0.5	-4.5	<0.0001
Time <sup>2</sup>	0.1	0.0	4.7	<0.0001
Fire*Time	-1.1	0.8	-1.5	0.13
Fire*Time <sup>2</sup>	0.0	0.0	1.5	0.14

The relative proportions of cover types found around the nests were significantly different (GLMM,  $F_{3,66} = 71.8$ ,  $P < 0.0001$ ). Herb cover was the highest and rock cover the lowest around *A. gibbosa* nests (Fig. 3). Although there was no global effect of fire (GLMM,  $F_{1,2} = 12.1$ ,  $P = 0.07$ ), there was a significant interaction



**Fig. 3.** Mean relative plant cover ( $\pm$ SE) of the different categories around *Aphaenogaster gibbosa* nests in the UB (white bars) and B (black bars) plots. Asterisks indicate significant differences between UB and B plots based on multiple comparison tests to which the Bonferroni correction was applied. Note that rock and litter cover were not included in the analysis.

between fire status and cover category (GLMM,  $F_{3,66} = 19.3$ ,  $P < 0.0001$ ). Nests located in B areas were surrounded by a higher proportion of bare ground, wood debris, and herb cover, whereas those located in UB areas had a higher proportion of shrub and litter cover (Fig. 3). Herb cover was not significantly different between B and UB areas.

The foraging distances of colonies in B and UB areas were not significantly different (mean  $\pm$  SE:  $0.82 \pm 0.05$  m and  $0.79 \pm 0.07$  m in B and UB plots, respectively; GLMM,  $F_{1,2} = 0.15$ ,  $P = 0.74$ ). Maximum foraging distances were 2.15 m and 2.28 m in B and UB plots.

#### Biotic conditions and diet

*Availability of food resources – arthropods and plant material.* Arthropod biomass did not differ significantly between B (mean  $\pm$  SE:  $0.03 \pm 0.00$  and  $105.8 \pm 19.6$  g per trap\*day of ground-dwelling and flying arthropods, respectively) and UB ( $0.03 \pm 0.04$  and  $71.2 \pm 14.6$  g per trap\*day of ground-dwelling and flying arthropods, respectively) areas (GLMM,  $F_{1,3} = 0.02$ ,  $P = 0.89$  and GLMM,  $F_{1,2} = 2.04$ ,  $P = 0.29$ , respectively). As for the availability of plant resources, there was no significant effect of fire on the total number of seeds in B

( $2637 \pm 823$  seeds  $m^{-2}$ ) and UB ( $2814 \pm 598$  seeds  $m^{-2}$ ) plots (GLMM,  $F_{1,2} = 0.11$ ,  $P = 0.7772$ ). Similarly, seed biomass was not different between B ( $2.4 \pm 0.6$ ) and UB ( $2.4 \pm 0.4$  g  $m^{-2}$ ) plots (GLMM,  $F_{1,2} = 0.02$ ,  $P = 0.91$ ). Seed assemblage composition, however, differed as a result of fire status (ANOSIM, Global  $R = 0.92$ ,  $P = 0.001$ ). SIMPER analysis showed that *Rosmarinus officinalis* was primarily responsible for these differences (total contribution of 29%), clearly accounting for more biomass in UB than B plots. *Argyrolobium zanonii*, *Aphyllantes monspeliensis*, and *Fumana ericoides* were also responsible for these differences (contributing > 10%), but they had more biomass in B than UB plots. Finally, the number of available petals was higher around nests in UB than B plots ( $\chi^2 = 20.7$ ,  $P < 0.0001$ , d.f. = 1) (Fig. 4a).

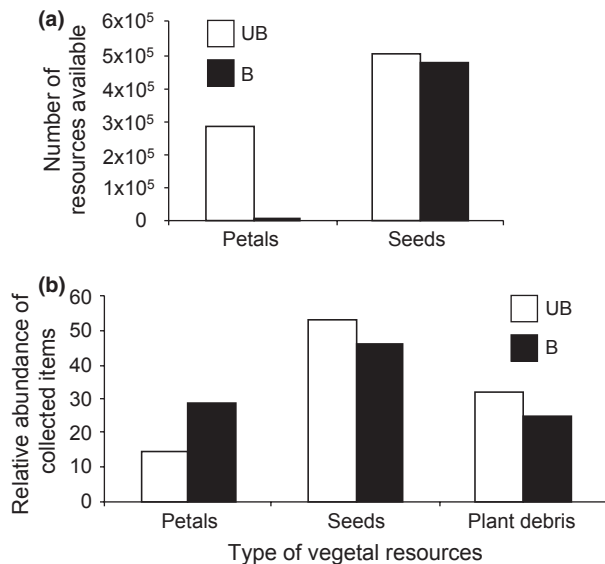
**Diet.** In accordance with the similarities in the amount of both plant and arthropod resources, there were no significant differences in either the relative dry weight (GLMM,  $F_{1,2} = 0.38$ ,  $P = 0.60$ ;  $26.5 \pm 7.2\%$ ) or the relative number of arthropod items (GLMM,  $F_{1,2} = 0.45$ ,  $P = 0.57$ ;  $46.0 \pm 4.6\%$ ) that composed the diet of *A. gibbosa*. The relative number of petals, seeds, and pieces of plant debris collected by *A. gibbosa*, however, was different in B and UB areas ( $\chi^2 = 7.3$ ,  $P = 0.027$ , d.f. = 2). In spite of the low availability of petals in B areas, petal collection was higher than in UB areas, whereas the collection of seeds and pieces of plant debris followed the opposite pattern (Fig. 4b). Furthermore, the relative contribution of seeds and petals to *A. gibbosa*'s diet was clearly different between B and UB areas. Its diet was mainly composed of seeds (Fig. 5a) and petals of *R. officinalis*

in UB areas; seeds (Fig. 5a) of *F. ericoides* and petals of the Cistaceae species (*F. ericoides* and *H. strictum*) as well as the Fabaceae species *A. zanonii* composed its diet in B areas. *Aphaenogaster gibbosa* did not collect the most abundant (and thus most available) seeds in B areas (Fig. 5b; Appendix S2). Note that the availability of *P. nigra* seeds was not estimated as we only sampled understory plant species.

## Discussion

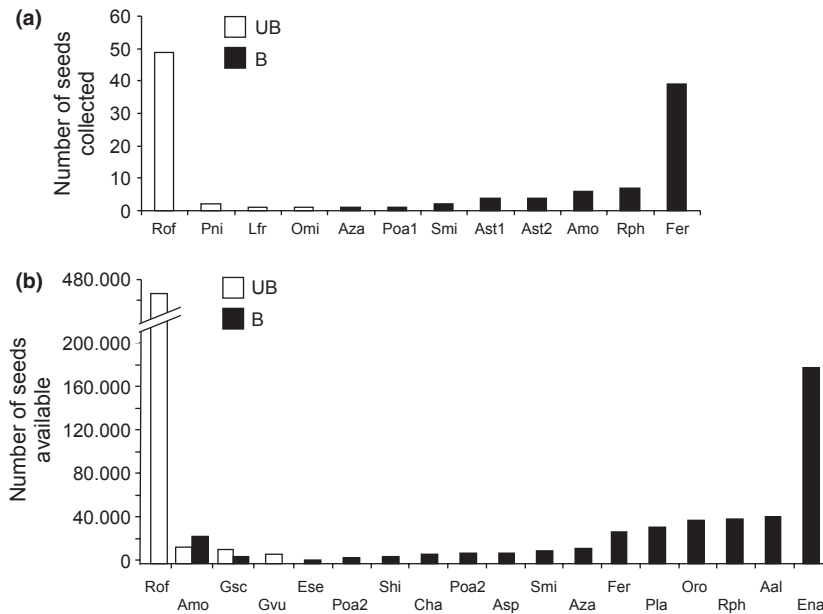
Even though the richness and abundance of ant species may remain unaltered after fire (e.g. Parr *et al.*, 2004; Arnan *et al.*, 2006), the mechanisms behind such responses may be species dependent. We found a similar number of colonies on B and UB plots 2 years after a fire, suggesting that *A. gibbosa* is resistant to the direct and indirect short-term effects of fire. First, *A. gibbosa*'s deep nests (30–40 cm; S. Caut, M.J. Jowers, X. Arnan, A. Rodrigo, X. Cerdá, R. Boulay, unpubl. data) may allow the species to survive fire as no heating occurs at such depths as long as the surface temperature is below 400 °C (DeBano, 2000). Other ant species, such as the harvester desert ant *Pogonomyrmex rugosus*, have also been shown to be resistant to fire (Zimmer & Parmenter, 1998). In the latter study, however, the experimental fires that were used to burn desert grasses were unlikely to attain the high temperatures associated with crown wildfires, such as the one that occurred in our study area. Second, and more interestingly, *A. gibbosa* foraging behaviour varied as a result of fire. In response to fire-induced changes in daily temperature cycles and food availability, this species adjusted not only its daily foraging activity but also the types of food resources it collected. As a result, *A. gibbosa* was able to maintain the same overall foraging activity and efficiency after the wildfire, which might explain why its abundance was unaffected (Arnan *et al.*, 2006; Rodrigo & Retana, 2006).

Canopy fires, such as the one that disturbed our study area, often completely remove vegetative cover. The vegetation, however, begins to recover within a few days (Traubaud & Lepart, 1980; Noble & Gill, 1981). The removal of cover and the speed of recovery have clear implications for environmental conditions important to ants, such as vegetative cover, microhabitat temperature, and food availability (Arnan *et al.*, 2007). Our burnt plots, which had burnt 2 years before, generally had less vegetative cover, an increased proportion of bare soil, and a total absence of leaf litter. Not surprisingly, these conditions resulted in more sun exposure on burnt plots and, consequently, higher midday temperatures for ants. Although daily temperature was clearly seasonal, we found few differences in daily plot temperatures and no differences in nest temperatures between burnt and unburnt areas. Both the wood debris present on burnt plots and the fast recovery of grass cover in this kind of forest (Rodrigo & Retana, 2006) could offset the lack of vegetative cover by providing some shade.



**Fig. 4.** (a) Overall number of seeds and petals available in the vicinity of *Aphaenogaster gibbosa* nests (25 m<sup>2</sup>) and (b) relative abundance of seeds, petals, and plant debris within the fraction of plant-based *A. gibbosa* dietary resources on UB (white bars) and B (black bars) plots.





**Fig. 5.** Species composition of seed items collected by *A. gibbosa* workers (a) versus their availability (b) on UB (white bars) and B (black bars) plots. For the purpose of comparison, values (both in the case of diet and availability) correspond to the summed number of seeds from all nests. Seed availability is only shown for those species contributing to more than 1% of total abundance. Abbreviations: Amo (*Aphyllantes monspeliensis*), Asp (*Astragalus* sp.), Aza (*Argyrolobium zanonii*), Cha (*Carex halleriana*), Ast1 (Asteraceae sp. 1), Ast2 (Asteraceae sp. 2), Ena (*Erucastrum nasturtiifolium*), Ese (*Euphorbia serrata*), Fer (*Fumana ericoides*), Poa1 (Poaceae sp. 1), Poa2 (Poaceae sp. 2), Gsc (*Genista scorpius*), Gvu (*Globularia vulgaris*), Lfr (*Lithospermum fruticosum*), Omi (*Ononis minutissima*), Oro (*Orobanchae* sp.), Pla (*Plantago lanceolata*), Pni (*Pinus nigra*), Rof (*Rosmarinus officinalis*), Rph (*Reseda phyteuma*), Shi (*Sideritis hirsuta*), Smi (*Sanguisorba minor*).

Plant community composition, and therefore the relative availability of seeds and petals, was clearly different between unburnt and burnt plots. For instance, the species that produced the most seeds on unburnt plots, *R. officinalis*, was absent from the burnt plots. Instead, the seeds most commonly found on burnt plots came from Fabaceae and Cistaceae species; these two plant families increase in abundance following fire in Mediterranean basin ecosystems (Ojeda *et al.*, 1996; Lloret & Vilà, 2003; De Luis *et al.*, 2006; Rodrigo *et al.*, 2012). The total number of petals was also higher in unburnt versus burnt areas. Despite these differences, however, total seed abundance, seed biomass, and arthropod biomass did not vary between unburnt and burnt areas.

As the fire had significantly modified abiotic and biotic conditions, *A. gibbosa*'s persistence on burnt plots was only possible because the species demonstrated behavioural flexibility, which allowed it to successfully forage in the new environment (Gordon, 1991). One of the most important findings of this study is that this species is able to maintain similar daily foraging activity in unburnt and burnt plots by adjusting its daily foraging activity to the new temperature patterns. In unburnt plots, colonies were active throughout the day, and activity decreased only slightly at noon. In contrast, activity in burnt areas decreased drastically, or even ceased, at midday (Appendix S1). This decrease was offset by an increase in

activity during the morning or the evening relative to the unburnt plots. As a result, this species had the same overall foraging activity in both unburnt and burnt plots because it was constantly active across a range of temperatures in unburnt areas, but was more active within a narrower range of favourable temperatures in burnt areas. This shift in daily activity parallels the pattern displayed by several Mediterranean ant species from spring to summer, as they cope with harsher summer temperatures, especially those at midday (Cerdá *et al.*, 1988; Cros *et al.*, 1997). Although not examined here, it may be that *A. gibbosa* shows summer activity rhythms in the spring on burnt plots, to cope with harsh environmental conditions.

The relative amount and dry weight of arthropod and plant items in *Aphaenogaster gibbosa*'s diet did not change. The species was equally omnivorous in unburnt and burnt plots, which fits with resource availability. A North American seed-harvesting ant species was found to collect more dead insects following fire (Zimmer & Parmenter, 1998), a behaviour that would match resource availability because fire kills many vegetation-dwelling insects. *Aphaenogaster gibbosa*, however, did not harvest resources in accordance with their availability. Although *Erucastrum nasturtiifolium* seeds were the most abundant seed type on burnt plots, ants favoured *Fumana ericoides* seeds. Also, although petals were less abundant in burnt areas, *A. gibbosa* exploited them more. Two different

hypotheses may explain this pattern. First, the abundance of seed-harvesting ant species may be enhanced by fire (Zimmer & Parmenter, 1998; Arnan *et al.*, 2006; Rodrigo & Retana, 2006). *Aphaenogaster gibbosa* ranks low in the dominance hierarchy of Mediterranean ant species (Arnan *et al.*, 2012), and inter-specific competition with seed-harvesting ants could force *A. gibbosa* to exploit petals at the expense of seeds. Nests, however, were evenly distributed on both burnt and unburnt plots, a pattern that highly suggests that intra-specific competition is at work (Levings & Traniello, 1981). If so, inter-specific competition may have less of an impact (Janzen, 1970; Connell, 1971) as *A. gibbosa* would face the fiercest competition from itself (among different colonies) (Boulay *et al.*, 2010), regardless of fire. Second, this preference for petals may reflect a pattern already observed for other *Aphaenogaster* species (Stager, 1923; Whitford *et al.*, 1980; Cerdá *et al.*, 1996; Wetterer *et al.*, 2002): *A. gibbosa* prefers petals when the habitat contains the types of petals it prefers, i.e. those of Cistaceae species (Cerdá *et al.*, 1988, 1996). The mechanisms that drive *Aphaenogaster* species to harvest this food resource still remain unknown.

Indeed, this dietary flexibility may also explain why foraging distances were not different for burnt and unburnt areas. Seed availability in burnt and unburnt areas was similar, even if seeds came from different species, and foragers could thus collect a plethora of resources without having to travel further from the nest. Moreover, the removal of vegetation and leaf litter by fire could facilitate foraging (Andersen, 1988; Jackson & Fox, 1996): petals and seeds may be easier to harvest in burnt plots, which have more bare ground. Indeed, reduced habitat structural complexity has enhanced food collection by ants elsewhere (Gibb & Parr, 2010). Because higher midday soil temperatures on burnt plots might constrain foraging, however, there may be a compromise between improved structural conditions and harsher thermal conditions. Overall, it would seem that *A. gibbosa* uses behavioural plasticity to adjust to post-fire environment: it modulates its daily foraging activity and changes the composition of its diet. Because this study was carried out just 2 years after the fire, however, we do not know if the short-term changes we observed will have negative, positive, or neutral consequences for long-term nest production and survival of this species. This question remains open and should be addressed in future research.

The few studies examining fire's effects on ant-activity patterns at the species level have found limited evidence that fire changes foraging; moreover, they were restricted to seed-harvesting species (McCoy & Kaiser, 1990; Zimmer & Parmenter, 1998). Fire was possibly found to have a limited impact because the species they examined inhabited sand hills (McCoy & Kaiser, 1990) or desert grasslands (Zimmer & Parmenter, 1998). These authors hypothesised that fire-induced environmental changes should be relatively greater in forested systems like ours. Our study demonstrates that fire-induced environmental changes, such as changes in temperature, plant cover, and food quality, can

affect the foraging activity of *A. gibbosa*. Our results also suggest that *A. gibbosa*'s behavioural plasticity and generalised diet help it cope with the conditions generated by the wildfire that burnt our study area. The high level of generalism among ant species (Hölldobler & Wilson, 1990) might thus explain why many ant communities are highly resilient to fire (e.g. Parr *et al.*, 2004; Arnan *et al.*, 2006). Species, however, differ in thermal tolerance and, consequently, their capacity to modulate their foraging patterns, which might account for their variable responses to fire. As fire has a highly variable effect on the resources used by insect species (e.g. Swengel, 2001; Moretti *et al.*, 2004, 2006; Arnan *et al.*, 2006, 2007; Barrow *et al.*, 2007; Rodrigo *et al.*, 2008; Schowalter, 2012), community responses are context dependent and thus seldom consistent. Increased knowledge about insects' functional responses to fire is needed, both for species that survive fire (like *A. gibbosa*) and for species that decline dramatically or disappear after fire. This information would greatly improve our understanding of and our ability to predict wildfire's effects on insect biodiversity, especially in fire-prone areas like the Mediterranean basin.

## Acknowledgements

We are very grateful to Irene Raya for field assistance, Miquel Riba for statistical advice, and Jessica Pearce-Duvet for English editing. This study was funded by the Spanish 'Ministerio de Ciencia e Innovación' project Consolider MONTES, CSD 2008-00040 to AR. All experiments comply with current Spanish laws.

## Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12018:

**Appendix S1.** Nest temperature and daily rhythms of ant activity in B and UB plots for the five observation days.

**Appendix S2.** Mean  $\pm$  SE seed density (seeds m<sup>-2</sup>) availability around *Aphaenogaster gibbosa* nests during this study.

## References

- Andersen, A.N. (1988) Immediate and longer-term effects of fire on seed predation by ants in sclerophyllous vegetation of south-eastern Australia. *Australian Journal of Ecology*, **13**, 285–293.
- Andersen, A.N. (1990) The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proceeding of the Ecological Society of Australia*, **16**, 347–357.
- Andersen, A.N. (1991a) Responses of ground-foraging ant communities to three experimental fire regimes in a savanna forest of tropical Australia. *Biotropica*, **23**, 575–585.

- Andersen, A.N. (1991b) Parallels between ants and plants: implications for community ecology. *Ant-Plant Interactions* (ed. by C.R. Huxley and D.F. Cutler), pp. 539–558. Oxford University Press, Oxford, UK.
- Andersen, A.N., Cook, G.D., Corbett, L.K., Douglas, M.M., Eager, R.W., Russell-Smith, J., Setterfield, S.A., Williams, R.J. & Woinarski, J.C.Z. (2005) Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. *Austral Ecology*, **30**, 155–167.
- Andersen, A.N., Hertog, T. & Woinarski, C.Z. (2006) Long-term fire exclusion and ant community structure in an Australian tropical savanna: congruence with vegetation succession. *Journal of Biogeography*, **33**, 828–832.
- Andersen, A.N., Penman, T.D., Debas, N. & Houadria, M. (2009) Ant community responses to experimental fire and logging in a eucalypt forest of south-eastern Australia. *Forest Ecology and Management*, **258**, 188–197.
- Arnan, X., Cerdá, X. & Retana, J. (2012) Distinctive life traits and distribution along environmental gradients of dominant and subordinate Mediterranean ant species. *Oecologia*, **170**, 489–500.
- Arnan, X., Rodrigo, A. & Retana, J. (2006) Post-fire recovery of Mediterranean ground ant communities follows vegetation and dryness gradients. *Journal of Biogeography*, **33**, 1246–1258.
- Arnan, X., Rodrigo, A. & Retana, J. (2007) Uncoupling the effects of shade and food resources of vegetation on Mediterranean ants: an experimental approach at the community level. *Ecography*, **30**, 161–172.
- Arnan, X., Rodrigo, A. & Retana, J. (2011) What are the consequences of ant-plant interactions on the abundance of two dry-fruited shrubs in a Mediterranean scrub? *Oecologia*, **167**, 1027–1039.
- Barrow, L., Parr, C.L. & Kohen, J.L. (2007) Habitat type influences fire resilience of ant assemblages in the semiarid tropics of Northern Australia. *Journal of Arid Environments*, **69**, 80–95.
- Bernadou, A. & Fourcassié, V. (2008) Does substrate coarseness matter for foraging ants? An experiment with *Lasius niger* (Hymenoptera; Formicidae). *Journal of Insect Physiology*, **54**, 334–342.
- Bernard, F. (1968) *Les fourmis (Hymenoptera Formicidae) d'Europe Occidentale et Septentrionale*. Collection Faune de l'Europe et du Bassin Méditerranéen, Masson, Paris, France.
- Boulay, R., Carro, F., Soriquer, R.C. & Cerdá, X. (2009) Small-scale indirect effects determine the outcome of a tripartite plant-disperser-granivore interaction. *Oecologia*, **161**, 529–537.
- Boulay, R., Galarza, J.A., Cheron, B., Hefetz, A., Lenoir, A., Van Oudenhove, L. & Cerdá, X. (2010) Intraspecific competition affects population size and resource allocation in an ant dispersing by colony fission. *Ecology*, **91**, 3312–3321.
- Brotons, L., Pons, P. & Herrando, S. (2005) Colonisation of dynamic Mediterranean landscapes: where do birds come from after fire? *Journal of Biogeography*, **32**, 789–798.
- Castaño-Meneses, G. & Palacios-Vargas, J.G. (2003) Effects of fire and agricultural practices on neotropical ant communities. *Biodiversity and Conservation*, **12**, 1913–1919.
- Centre de Recerca Ecològica i Aplicacions Forestals (CREAF) (2010) Mapa de cobertes del sòl de Catalunya (MCSC). <<http://www.creaf.uab.cat/mcsc/>> 6th June 2011.
- Cerdá, X., Bosch, J., Alsina, A. & Retana, J. (1988) Dietary spectrum and activity patterns of *Aphaenogaster senilis* (Hymenoptera: Formicidae). *Annales de la Société Entomologique de France*, **24**, 69–75.
- Cerdá, X., Retana, J., Carpintero, S. & Cros, S. (1996) An unusual ant diet: *Cataglyphis floricola* feeding on petals. *Insectes Sociaux*, **43**, 101–104.
- Clark, P.J. & Evans, F.C. (1954) Distance to nearest neighbour as a measure of spatial relationships in populations. *Ecology*, **35**, 445–453.
- Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117–143.
- Clarke, K.R. & Gorley, R.N. (2001) *PRIMERv5: User Manual/Tutorial*. PRIMER-E, Plymouth, UK.
- Clay, N.A., Bauer, M., Solis, M. & Yanoviak, S.P. (2010) Arboreal substrates influence foraging in tropical ants. *Ecological Entomology*, **35**, 417–423.
- Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of Populations* (ed. by P.J. Den Boer and G. Gradwell), pp. 298–312. PUDOC, Wageningen, the Netherlands.
- Cros, S., Cerdá, X. & Retana, J. (1997) Spatial and temporal variation in the activity patterns of Mediterranean ant communities. *Ecoscience*, **4**, 269–278.
- De Luis, M., Raventós, J. & González-Hidalgo, J.C. (2006) Post-fire vegetation succession in Mediterranean gorse shrublands. *Acta Oecologica*, **30**, 54–61.
- DeBano, L.F. (2000) The role of fire and soil heating on water repellency in wildland environments: a review. *Journal of Hydrology*, **231–232**, 195–206.
- Farji-Brener, A.G., Corley, J.C. & Bettinelli, J. (2002) The effects of fire on ant communities in north-western Patagonia: the importance of habitat structure and regional context. *Diversity and Distributions*, **8**, 235–243.
- Folgarait, P.J. (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation*, **7**, 1221–1244.
- Folkerts, G.W., Deyrup, M.A., Sisson, D.C. (1993) Arthropods associated with xeric longleaf pine habitats in the southeastern United States: a brief overview. *The Longleaf Pine Ecosystems. Ecology, Restoration and Management* (ed. by S.M. Hermann), pp. 159–203. Proceedings of the Tall Timber Fire Ecology Conference, No. 18. Tall Timbers Research Station, Tallahassee, Florida.
- Frizzo, T.L.M., Campos, R.I. & Vasconcelos, H.L. (2012) Contrasting effects of Fire on Arboreal and Ground-Dwelling Ant Communities of a Neotropical Savanna. *Biotropica*, **44**, 254–261.
- Gibb, H. & Parr, C.L. (2010) How does habitat complexity affect foraging success? A test using functional measures on three continents. *Oecologia*, **164**, 1061–1073.
- Gill, A.M., Groves, R.H. & Noble, I.R. (1981) *Fire and the Australian Biota*. Australian Academy of Science, Canberra, South Australia.
- Gordon, D.M. (1991) Behavioral flexibility and the foraging ecology of seed-eating ants. *American Naturalist*, **138**, 379–411.
- Hölldobler, B. & Wilson, E.O. (1990) *The Ants*. Springer, Berlin, Germany.
- Jackson, G.P. & Fox, B.J. (1996) Comparison of regeneration following burning, clearing or mineral sand mining at Tomago, NSW: II. Succession of ant assemblages in a coastal forest. *Australian Journal of Ecology*, **21**, 200–216.

- Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist*, **104**, 501–528.
- Levings, S. & Traniello, J.F.A. (1981) Territoriality, nest dispersion and community structure in ants. *Psyche*, **88**, 265–319.
- Lloret, F. & Vilà, M. (2003) Diversity patterns of plant functional types in relation to fire regime and previous land use in Mediterranean woodlands. *Journal of Vegetation Science*, **14**, 387–398.
- McCoy, E.D. & Kaiser, B.W. (1990) Changes in foraging activity of the southern harvester ant *Pogonomyrmex badius* (Latreille) in response to fire. *American Midland Naturalist*, **123**, 112–123.
- Moretti, M., Duelli, P. & Obrist, M.K. (2006) Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests. *Oecologia*, **149**, 312–327.
- Moretti, M., Obrist, M.K. & Duelli, P. (2004) Arthropod biodiversity after forest fires: winners and losers in the winter fire regime of the Southern Alps. *Ecography*, **27**, 173–186.
- Noble, I.R. & Gill, A.M. (1981) Dynamics and evolution of the Australian vegetation under the impact of fire. Meeting of the 13th international botanical congress, Sydney, NSW. August, 21–28.
- Ojeda, F., Marañón, T. & Arroyo, J. (1996) Postfire regeneration of a mediterranean heathland in Southern Spain. *International Journal of Wildland Fire*, **6**, 191–198.
- Paquin, P. & Coderre, D. (1997) Deforestation and fire impact on edaphic insect larvae and other macroarthropods. *Environmental Entomology*, **26**, 21–30.
- Parr, C.L., Robertson, H.G., Biggs, H.C. & Chown, S.L. (2004) Response of African savanna ants to long-term fire regimes. *Journal of Applied Ecology*, **41**, 630–642.
- Pastro, L.A., Dickman, C.R. & Letnic, M. (2011) Burning for biodiversity or burning biodiversity? Prescribed burn vs. wild-fire impacts on plants, lizards, and mammals. *Ecological Applications*, **21**, 3238–3253.
- R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org>> 6th June 2011.
- Retana, J., Picó, F.X. & Rodrigo, A. (2004) Dual role of harvesting ants as seed predators and dispersers of a non-myrmecochorous Mediterranean perennial herb. *Oikos*, **105**, 377–385.
- Rodrigo, A., Arnan, X. & Retana, J. (2012) Relevance of soil seed bank and seed rain on seed supply after a large wildfire. *International Journal of Wildland Fire*, **21**, 449–458.
- Rodrigo, A. & Retana, J. (2006) Post-fire recovery of ant communities in Submediterranean *Pinus nigra* forests. *Ecography*, **29**, 231–239.
- Rodrigo, A., Sardà-Palomera, F., Retana, J. & Bosch, J. (2008) Changes of dominant ground beetles in black pine forests with fire severity and successional age. *Ecoscience*, **15**, 442–452.
- Schowalter, T.D. (2012) Insect responses to major landscape-level disturbance. *Annual Review of Entomology*, **57**, 1–20.
- Stager, R. (1923) Resultate meiner Beobachtungen und Versuche an *Aphaenogaster testaceo-pilosa* Lucas, *spinosa* Emery var. *nitida* Emery. *Zeitsch. Zeitschrift für Wissenschaftliche Insektenbiologie*, **18**, 351–356.
- Sundstrom, L. (1993) Foraging responses of *Formica truncorum* (Hymenoptera: Formicidae): exploiting stable vs. spatially and temporally variable resources. *Insectes Sociaux*, **40**, 147–161.
- Swengel, A.B. (2001) A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodiversity and Conservation*, **10**, 1141–1169.
- Trabaud, L. & Lepart, J. (1980) Diversity and stability in garrigue ecosystems after fire. *Vegetatio*, **43**, 49–57.
- Traniello, J.F.A. (1989) Foraging strategies of ants. *Annual Review of Entomology*, **34**, 191–210.
- Wetterer, J.K., Himler, A.G. & Yospin, M.M. (2002) Forager size, load size, and resource use in an omnivorous ant, *Aphaenogaster albisetosa* (Hymenoptera: Formicidae). *Sociobiology*, **39**, 335–343.
- Whelan, R.J. (1995) *The ecology of fire*. Cambridge University Press, New York, New York.
- Whitford, W.G., Depree, E. & Johnson, P. (1980) Foraging ecology of two Chihuahuan desert ant species: *Novomessor cockerelli* and *Novomessor albisetosus*. *Insectes Sociaux*, **27**, 148–156.
- York, A. (1994) The long-term effects of fire on forest ant communities: management implications for the conservation of biodiversity. *Memoirs of the Queensland Museum*, **36**, 231–239.
- Zimmer, K. & Parmenter, R.R. (1998) Harvester ants and fire in a desert grassland: ecological responses of *Pogonomyrmex rugosus* (Hymenoptera: Formicidae) to experimental wildfires in central New Mexico. *Environmental Entomology*, **27**, 282–287.