

## The impact of macro- vs. micro-environmental factors on the structure of ant communities inhabiting East-Mediterranean Aleppo pine forests

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### ABSTRACT

This study set out to elucidate the mechanisms structuring ant species composition in an Aleppo pine (*Pinus halepensis*) forest on Mount Carmel, Israel, and to reveal the forces that maintain species diversity on the macro- and micro-scale levels. Ants were sampled by pitfall traps during all four seasons at three forest stands that differed in time elapsed since the last forest fire. The studied macro-environment factors were fire and season, while the micro-environment factors were plant species, leaf litter, and microclimate conditions. Fires had a short- and medium-term positive effect on ant species richness by promoting ant biodiversity and maintaining habitat heterogeneity. Cluster analysis revealed that the effects of fire were far less important predictors of ant community structure than seasonality when comparing 1- and 14-year post-fire stands, but that the time elapsed since the fire was much more important than season when comparing unburned to burned stands. Different ant functional groups responded to fire in strikingly opposite ways: opportunistic species (e.g., *Tetramorium* spp., *Aphenogaster* spp.) were affected more severely than other functional groups and their proportion decreased with post-fire succession. Generalist Myrmicinae (e.g. *Pheidole* spp., *Monomorium* spp.), on the other hand, benefited from fire and their proportion increased with post-fire succession. A novel finding in this study was that the microhabitat beneath the canopy of different plant species (*P. halepensis*, *Cistus* sp., *Quercus calliprinos*, and *Pistacia lentiscus*) in the unburnt forest provided different environmental conditions and was thus inhabited by unique ant communities. We conclude that maintaining habitat heterogeneity on both the micro- and macro-scale levels is essential for the restoration of ant biodiversity on Mount Carmel.

**KEYWORDS:** fire, season, vegetation, *Pinus halepensis*, micro-habitat, soil temperatures, soil moisture, *Pistacia lentiscus*, *Quercus calliprinos*, *Cistus* sp., functional groups, species richness

## INTRODUCTION

Understanding the factors that determine the distribution and abundance of organisms in their natural habitats is a major goal in ecological studies. It is widely acknowledged that community structure is affected by a myriad of abiotic and biotic factors, with the relative importance of each often depending on the temporal and spatial scale of study (Levin, 1992). The study of spatio-temporal patterns is crucial not only for understanding the causes of the distribution and abundance of organisms but also for providing a basis for monitoring any long-term changes arising from both natural and human disturbances (e.g., Robertson et al., 1993). Here, we studied the community structure of litter- and soil-dwelling ants in a natural Aleppo pine (*Pinus halepensis*) forest in the East-Mediterranean region along two spatio-temporal scales: a regional scale with respect to time elapsed since a fire event, and a season and microhabitat scale with respect to the environment established beneath the canopies of specific plant species, including leaf litter and microclimate conditions in different seasons.

Spatial and temporal variability in ant assemblages have been attributed to different biological and/or physical factors, primarily habitat disturbance, vegetation attributes, and competitive interactions (Andersen, 1995). Perturbations such as fire occur across all spatio-temporal scales and are major drivers of community structure, especially in areas under intensive anthropogenic activity such as the Mediterranean region (Collins and Smith, 2006). The effect of different disturbances on ant biodiversity was reviewed by Folgarait (1998), who concluded that it generally increases after fire. However, post-fire ant diversity may also decrease (e.g. Majer, 1977; York, 2000; Ratchford et al., 2005) or remain unchanged (e.g. Majer, 1977; Jackson and Fox, 1996; Hoffmann, 2003; Parr et al., 2004; Rodrigo and Retana, 2006), depending on biotic and abiotic conditions, fire frequency and intensity, and time elapsed since the fire event (York, 2000; Izhaki et al., 2003). Although the flora and fauna of Mediterranean ecosystems are assumed to be highly adapted to frequent fires (Naveh, 1999), only a few studies have provided support for this assumption in relation to ant community structure in these ecosystems (Abel and Pons, 1998; Arnan et al., 2006; Rodrigo and Retana, 2006).

Natural seasonal cycles of abiotic factors, such as moisture and temperature, may also impose temporal changes upon ant communities (Hölldobler and Wilson, 1990). In a longleaf pine forest in Florida, the effects of season on ant community composition were more dominant than those of fire (Izhaki et al., 2003). Although seasonal activity cycles in ants were documented in the past (Fellers, 1989; Suarez et al., 1998; Izhaki et al., 2003), activity patterns of entire ant assemblages throughout the annual cycle have been largely overlooked (but see Fellers, 1989; Prusak, 1997; Albrecht and Gotelli, 2001).

On the regional and community-wide scales, ground-dwelling ant community composition has been associated with a variety of variables related to plants, including vegetation cover (Greenslade and Greenslade, 1977; Retana and Cerdá, 2000; Corley et al., 2006), vegetation composition (Gotelli and Ellison, 2002; Ratchford et al., 2005), vegetation productivity (Kaspari et al., 2000), plant species richness (Hoffmann et al., 2000; Ellison et al., 2002; Boulton et al., 2005), types of post-fire vegetation resilience (Arnan et al., 2006), plant biomass (Boulton et al., 2005), and vegetation architecture

(Hill et al., 2008). However, the effect of a specific plant species on ant community composition, particularly through attributes of the microhabitat established beneath its canopy, has been largely overlooked (see Doblás-Miranda et al., 2009).

The major aim of this study was to examine the spatio-temporal variability in ant community structure in relation to environmental factors. We examined the hypothesis that ant community structure at any given site on Mt. Carmel can be predicted from both macro- and micro-scale variables. Hence, we examined concomitantly the spatial and temporal ant community structure in an area on Mount Carmel using these two scales. The macro-scale was at the landscape-regional level and included the impacts of time elapsed since a fire event, and seasonality. The micro-scale focused on the microhabitat level and included defined areas beneath the canopy of four plant species where environmental conditions such as leaf litter and microclimate were determined in order to reveal their role in shaping the ant community in the unburnt forest.

## MATERIALS AND METHODS

### Study site

The study was conducted in a natural Aleppo pine (*Pinus halepensis*) forest on Mount Carmel, Israel, where the climate is typically Mediterranean with a mean annual rainfall of 600–700 mm, mainly during December–February, and with a long, hot, and dry period during May–October. Mean temperature in the coldest month (January) is 12 °C and in the warmest month (August) 26 °C (Atlas of Israel, 1970). Major parts of the natural forest have been disturbed by manmade fires for many decades and much effort has been dedicated to its restoration by the local forestry authorities. The density of *P. halepensis* trees in unburnt forests on Mount Carmel ranges from 19 to 55 trees per 1000 m<sup>2</sup>, with a height range of 5.9–14 m (Schiller et al., 1997). The understory in the natural pine forests on Mt. Carmel is composed mainly of small trees (e.g., *Quercus calliprinos* and *Pistacia palaestina*), shrubs (e.g., *Pistacia lentiscus*), and climbers (e.g., *Smilax aspera* and *Clematis cirrhosa*). Shrubby patches, dominated mainly by *Cistus* sp., and gaps composed mainly of herbaceous vegetation, occur among the pine trees (Laster, 2005). Post-fire regeneration of the natural Aleppo pine forest in this region was described by Ne'eman (1997), Schiller et al. (1997), and Arianoutsou and Ne'eman (2000). In the first part of the study, we examined the effect of time elapsed since a fire event and of season on ant-community structure. To that end, we selected three Aleppo pine (*P. halepensis*) forest stands located within a 10 × 10-km area on Mt. Carmel, Israel. An effort was made to select three stands that were as homogeneous as possible. All stands were on chalky marls with typical yellow rendzina soils. All stands were 340–420 m asl and their slopes were <10°. The first two stands represented a chronosequence of 1 and 14 years since the last fire event, while the control stand had had no fire record for at least 70 years (Schiller et al., 1997).

In the second part of the study, carried out in the control stand, we examined whether the understory of different plant species constituted different microhabitats with specific environmental conditions, conducive to unique ant communities in these areas.

### Ant sampling

We sampled ants with pitfall traps in two stages. First, we randomly set 20 traps per 400 m<sup>2</sup> at each of the three stands during 2003–2004. We retrieved the traps every three days and carried out 30 trapping sessions per season (summer and winter), 10 for each of the three stands. Second, at the control stand we placed traps beneath the canopy of four common plant species (*P. halepensis*, *Q. calliprinos*, *P. lentiscus*, and *Cistus* sp.), 1 trap under each of 10 randomly selected individuals of each plant species. An effort was made to ensure that sampling represented the intra-site variation, including the different slopes and aspects. Although the three stands selected for this study represented a post-fire chronosequence, the variation in ant presence among the stands may have originated from a variation in other environmental factors than forest age. Furthermore, a robust statistical analysis of time-since-fire effects demands replicates from each post-fire age, which unfortunately are not available under a natural fire regime. Thus, sampling from different slopes provided a minimum level of replication over the chronosequence. The traps were retrieved every seven days and trapping sessions were carried out twice per season (winter, spring, summer, and fall) during 2004–2005. The traps were constructed from 30-ml plastic cups (2 cm in diameter) embedded in the soil so that the lip of the cup was flush with the soil surface. Cups were partially filled with a 50:50 mixture of propylene glycol and water. The contents of the traps were stored in 70% ethanol until identification. Pitfall traps provide a good estimate of the relative abundance of an ant species foraging on the ground (Romero and Jaffe, 1989). Ant identification was carried out by Y. Ofer, based on Menozzi (1933), Tohmé (1969) and Kugler (1984), and nomenclature is consistent with Bolton (1995) and Kugler (1984).

### Environmental conditions

Air temperature, soil temperature, air humidity, and soil moisture were recorded for each microhabitat at each ant-sampling session. Soil moisture was measured at a 10-cm depth using a WET (WET1, Delta-T Devices Ltd, Cambridge, UK) and moisture meter (HH2, Delta-T Devices Ltd, Cambridge, UK). During each ant-sampling session, dry litter on the forest floor under each of the plant species was collected from an area of 324 cm<sup>2</sup> and oven-dried at 70 °C until a constant weight was obtained over two weeks.

### Functional groups

All ant species were classified into functional groups based on the effects of environmental stresses and disturbances on an ant species according to Andersen (1991, 1995) and Brown (2000). The classification scheme is based on habitat requirements and competitive interactions. Previous studies demonstrated that the ant functional group approach enabled a comparison of responses of ant communities to a variety of disturbances (e.g., Gómez et al., 2003; Izhaki et al., 2003). Ants on Mount Carmel belong to six functional groups: opportunists (unspecialized and poorly competitive, rapidly colonize disturbed areas); generalist Myrmicinae (unspecialized but highly competitive);

associated subordinate Camponotini (usually large species, coexisting successfully with dominant species); cryptic species (nest and forage predominantly in soil and litter and rarely interact with other species); hot climate specialists (species adapted to arid conditions and avoid dominant Dolichoderinae); and cold climate specialists (species typical of cooler conditions found in areas with a few dominant Dolichoderinae).

## Data analysis

### *The effect of fire and season on ant community structure*

The impacts of fire and season on the differences in species richness among the three forest stands were assessed using two-way ANOVA. Bonferroni post hoc tests were used to compare differences among stands. We applied the widely-used Sørensen similarity index (Magurran, 2004) to measure similarity in species composition between two sites with the equation  $Q_s = 2c/(a + b)$ , where  $a$  is the number of species found at site A,  $b$  the number of species at site B, and  $c$  the number of species shared by the two sites. We used the hierarchical method in cluster analysis to identify groups of habitats (control, 1- and 14-years post-fire) and season (winter and summer) that were similar in terms of ant species composition. The results are presented in a dendrogram in which habitats and seasons that are more similar in terms of species composition group more closely together. The dendrogram was constructed based on the Squared Euclidean between pairs.

### *Effect of microhabitat and season on ant community-structure*

Differences in microclimate conditions, seasons, species richness, diversity, and abundance among the four microhabitats (plant species) were analyzed by one- and two-way ANOVA followed by Bonferroni post hoc tests ( $p < 0.05$ ). We calculated Simpson's diversity index, one of the most robust and easily interpreted methods (Magurran, 2004), which measures the probability of picking two organisms of different species at random. Simpson's index ranges from 1.0, representing one species within the habitat, to a higher number, representing greater species diversity. Normal distribution was analyzed prior to statistical tests using the Shapiro–Wilk test. All statistical calculations were performed using the Statistical Package for the Social Sciences (version 12; SPSS, 2004). However, since previous studies demonstrated that sampling of insect communities rarely accounts for all species present (Colwell, 2006), in order to estimate asymptotic true species richness we used the Chao1 index, a non-parametric, abundance-based estimator based on the occurrence of singleton and doubleton species (Chao, 1984). This estimator was found appropriate for studies with a relatively uniform sample size and collection method, and had the best performance among 15 species-richness estimators of arthropod communities (Hortal et al., 2006). For the calculations, we treated each pitfall trap as a sample, as done in other studies of this kind (e.g., Colwell et al., 2004; Ratchford et al., 2005). Chao1 was calculated using EstimateS version 8.0 (Colwell, 2006).

To investigate ant assemblage composition in relation to environmental variables (stands with different fire history, season, plant species, microclimatic conditions, leaf litter), Canonical Correspondence Analysis (CCA) was performed using CANOCO 4.5 (Ter Braak and Smilauer, 2002). This method permits the construction of theoretical

variables (ordination axes) that best fit the species data according to a unimodal method of ordination. In the canonical ordination these axes constitute a linear combination of environmental variables. The correlations between environmental variables and ordination axes are derived and summarized in the eigenvalue of the ordination axis. The result of CCA is a set of scores for both sites and taxa, which can be presented as a two-dimensional ordination diagram where points represent sites or taxa, and arrays outgoing from the origin express environmental variables (Ter Braak and Smilauer, 2002). The length of the arrays represents the importance of the respective variable. The data were not transformed and species were not down-weighted. The statistical significance of the relationship between all species and all variables was tested by the Monte Carlo permutation test using 999 permutations (Ter Braak and Smilauer, 2002).

## RESULTS

### Effect of fire and season on ant community structure

A total of 40 ant species was recorded in the three forest stands representing the time elapsed since fire (Table 1). In summer, species richness per trapping session at the stand 14-years post-fire was significantly greater than at the control stand but similar to the 1-year post-fire stand (Fig. 1). No significant difference in species richness per trapping session was detected among the three stands in winter. Two-way ANOVA revealed that the time elapsed since fire significantly affected species richness per trapping session ( $F_{2,54} = 3.32, p < 0.05$ ); whereas season had no significant effect on species richness ( $F_{1,54} = 2.74, p > 0.05$ ). Thus, we pooled the two seasons and found a difference in species richness among the three stands (1-year post-fire:  $2.95 \pm 0.44$ , 14-years post-fire:  $3.25 \pm 0.44$ , unburnt:  $1.75 \pm 0.44$ ,  $F_{2,57} = 3.2, p < 0.05$ ), stemming from a significant difference between the 14-years post-fire and the unburnt stands (Bonferroni multiple comparison,  $p < 0.05$ ).

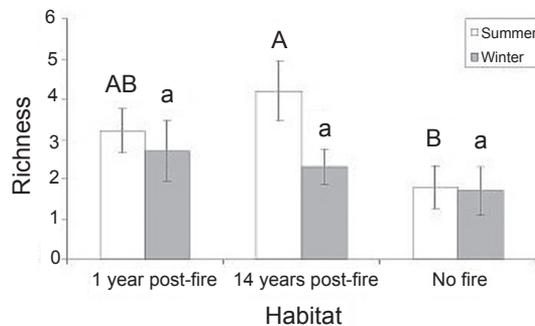


Fig. 1. Ant species richness (mean  $\pm$  1 SE) per trap per trapping session in each season in three habitats that differ in the time elapsed since a fire event on Mount Carmel, Israel (one-way ANOVA, summer:  $F_{2,27} = 3.82, p < 0.05$ ; winter:  $F_{2,27} = 0.67, p > 0.05$ ). Bars labeled with the same letter (Summer: capital letters, Winter: lowercase letters) are not significantly different (Bonferroni post hoc test,  $p > 0.05$ ).

Table 1

Classification into functional groups (after Andersen 1991, 1995) of ant species collected from three habitats that differ in the time elapsed since a fire event on Mount Carmel, Israel. Species that appeared only in one habitat are highlighted in light gray and those that appeared in at least two habitats are highlighted in dark gray

Species	Functional group	1-year post-fire	14-year post-fire	Unburnt
<i>Tetramorium meridionale</i>	OP	Light gray		
<i>Tetramorium punicum</i>	OP	Light gray		
<i>Monomorium abeillei</i>	GM			
<i>Tetramorium caespitum</i>	OP	Light gray		
<i>Aphaenogaster schmitzi</i>	OP	Light gray		
<i>Cataglyphis viaticoides</i>	HC	Light gray		
<i>Tetramorium signatum</i>	OP	Dark gray		
<i>Paratrechina longicornis</i>	OP	Dark gray		
<i>Lepisiota bipartita</i>	OP	Dark gray		
<i>Cardiocondyla emeryi</i>	OP	Dark gray		
<i>Monomorium subopacum</i>	GM		Light gray	
<i>Tetramorium sahlbergi</i>	OP		Light gray	
<i>Tetramorium sp.</i>	OP		Light gray	
<i>Tetramorium striativentre</i>	OP		Light gray	
<i>Crematogaster jehovae</i>	GM		Light gray	
<i>Crematogaster nigriceps</i>	GM		Light gray	
<i>Lepisiota syriaca</i>	OP		Light gray	
<i>Pheidole sinaitica</i>	GM		Light gray	
<i>Messor herbraeus</i>	HC		Light gray	
<i>Messor dentatus</i>	HC		Light gray	
<i>Cataglyphis sp.</i>	HC		Dark gray	
<i>Tapinoma simrothi</i>	OP		Dark gray	
<i>Aphaenogaster splendida</i>	OP		Dark gray	
<i>Crematogaster scutellaris</i>	GM		Dark gray	
<i>Plagiolepis ancyrensis</i>	OP		Dark gray	
<i>Lasius alienus</i>	CC		Dark gray	
<i>Cardiocondyla nuda</i>	OP		Dark gray	
<i>Monomorium pallidum</i>	GM		Dark gray	Light gray
<i>Monomorium dentigerum</i>	GM		Dark gray	Light gray
<i>Aphenogaster subterradians</i>	OP		Dark gray	Light gray
<i>Aphenogaster splendens</i>	OP		Dark gray	Light gray
<i>Camponotus truncatus</i>	SC		Dark gray	Light gray
<i>Crematogaster ionia</i>	GM		Dark gray	Light gray
<i>Pheidole teneriffana</i>	GM		Dark gray	Light gray
<i>Pheidole pallidula</i>	GM		Dark gray	Light gray
<i>Cataglyphis frigidus</i>	HC		Dark gray	Light gray
<i>Monomorium niloticum</i>	GM	Dark gray	Dark gray	Dark gray
<i>Camponotus fellah</i>	SC	Dark gray	Dark gray	Dark gray
<i>Crematogaster jehovae</i>	GM	Dark gray	Dark gray	Dark gray
<i>Lepisiota splendens</i>	OP	Dark gray	Dark gray	Dark gray

CR—cryptic, CC—cold climate, GM—generalist Myrmicinae, HC—hot climate, OP—opportunists, SC—subordinate Camponotini.

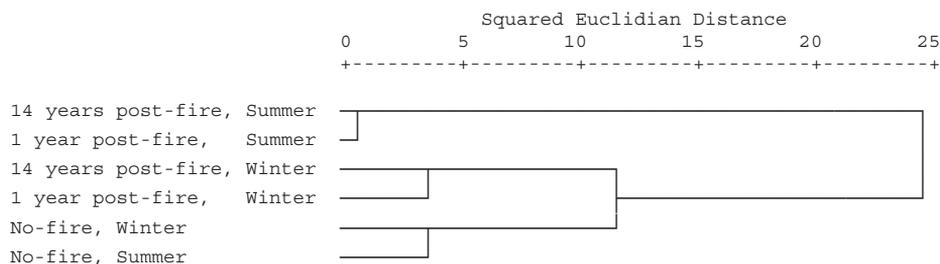


Fig. 2. Dendrogram showing the results of a cluster analysis illustrating the degree of similarity between the three habitats for two seasons according to their species composition.

Ant community composition (pooled seasons) of the two post-fire stands were more similar to each other (Sorensen index,  $Q_s = 0.4$ ) than to the control (1-year post-fire stands,  $Q_s = 0.24$ ; 14-years post-fire stands,  $Q_s = 0.36$ ). The time elapsed since a fire event was less important than season in shaping ant community structure when comparing the 1- and 14-years post-fire stands (Fig. 2). However, this was not the case for the control stand, where the differences between winter and summer in ant community composition were less dominant than those governed by time elapsed since fire (Fig. 2). Moreover, the 14-years post-fire stand had the largest number of unique species (12), i.e., those that did not inhabit any of the other two stands, whereas the lowest number of unique species (6) was detected in the 1-year post-fire stand (Table 1). Only four ant species inhabited all three stands (Table 1).

The two richest functional groups in the three stands were opportunists (19 species) and generalist Myrmicinae (13 species) (Table 1). The fraction of opportunistic species decreased with the time elapsed since fire from 64% in the 1-year post-fire stand to 43% in the 14-years post-fire stand and 23% in the control. The generalist Myrmicinae showed an opposite trend, with increased percentage as time elapsed since fire, with 21%, 33%, and 54% in the 1-year, 14-years since fire, and control stand, respectively. The other four functional groups were much less abundant, with five species being hot-climate specialists, two species being subordinate Camponotini and cryptic, and only one species being a cold-climate specialist (Table 1).

### Effect of microhabitat on ant community structure

The microhabitats established beneath the four plant species in the control stand differed in several abiotic conditions. Mean annual soil moisture beneath *Q. calliprinos* was 25%–76% higher compared with the other three plant species (although the difference from the *Cistus* microhabitat was not significant (Fig. 3)). Mean annual soil temperature beneath *Q. calliprinos* was 6%–10% lower compared with the other three plant species (although the difference was significant only in the *P. lentiscus* microhabitat (Fig. 3)). Mean annual air humidity and temperature did not differ significantly among the four microhabitats ( $F_{3,236} = 0.43$ ,  $p > 0.05$  and  $F_{3,276} = 2.16$ ,  $p > 0.05$ , respectively). In addi-

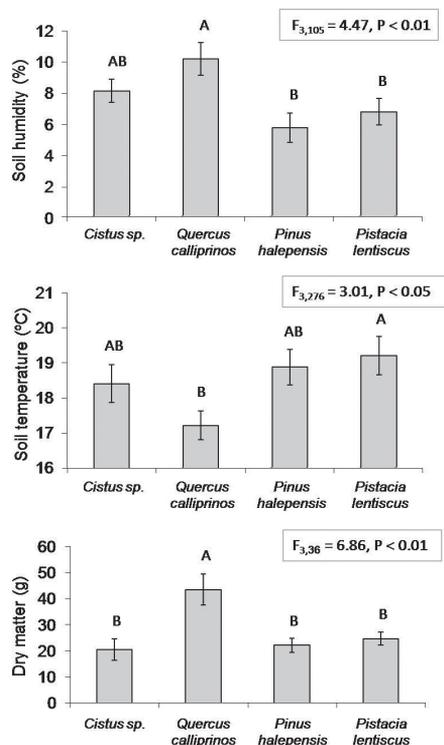


Fig. 3. Soil moisture, soil temperature and dry matter (mean  $\pm$  SE) under the canopy of four plant species in Mount Carmel, Israel. Differences among microhabitats were analyzed by one-way ANOVA. Bars labeled with the same letter are not significantly different (Bonferroni post hoc test,  $p > 0.05$ ).

tion, dry organic matter was 76%–112% higher beneath the canopy of *Q. calliprinos* compared with the other microhabitats (Fig. 3).

A total of 34 ant species were trapped during all four seasons in the four microhabitats, whereas the Chao1 estimate for the total richness for all microhabitats for all seasons was  $37.5 \pm 3.5$  (SD) species. Both mean species richness and mean species diversity per pitfall trap did not differ among the four microhabitats but were significantly affected by season (Table 2): in all four microhabitats the highest richness and diversity were observed in summer and the lowest in winter. Total ant abundance per trap was significantly affected by both season and microhabitat (Table 2), with greater abundances beneath the *Cistus sp.* canopy in summer. Chao1 calculations revealed significant differences in estimated species richness among the four microhabitats (one-way ANOVA,  $F_{3,307} = 64.3$ ,  $p < 0.001$ ); in the *P. lentiscus* microhabitat, 17 species were sampled, with a Chao1 estimate of  $18.6 \pm 2.2$  (SD). In the *Cistus* microhabitat, 21 species were sampled, with a Chao1 estimate of  $27.1 \pm 6.1$  species. In the *Quercus calliprinos* microhabitat, 12 species were sampled, with a Chao1 estimate of  $24.5 \pm 17.1$  species. In the *Pinus*

Table 2  
 Results of two-way analysis of variance (ANOVA) for ant species richness, species diversity (Simpson index), and total abundance per pitfall trap. Fixed factors: microhabitat (under four plant species: *Quercus calliprinos*, *Pistacia lentiscus*, *Pinus halepensis*, and *Cistus* sp.) and season (spring, summer, fall, and winter)

Source of variation	df	Species richness			Species diversity			Total abundance		
		MS	F	P	MS	F	P	MS	F	P
Microhabitat	3	1.26	1.52	0.21	0.18	0.30	0.83	254.6	5.42	0.01
Season	3	56.91	68.68	0.001	31.51	52.55	0.001	1046.9	22.30	0.001
Microhabitat × Season	9	1.70	1.53	0.14	0.80	1.33	0.22	163.6	3.49	0.001
Error	293	0.83			0.60			46.9		

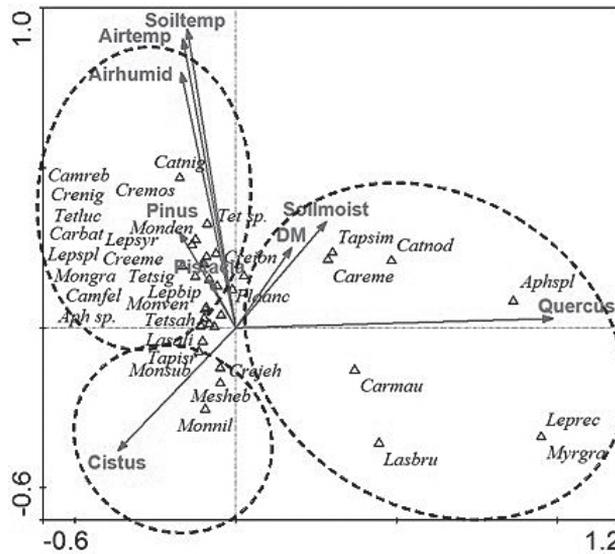


Fig. 4. Species-environment b-plot based on a canonical correspondence analysis (CCA) for the effect of environmental factors (represented by arrows): four microhabitats established under the canopy of four plant species (*Quercus calliprinos*, *Pistacia lentiscus*, *Pinus halepensis*, and *Cistus* sp.) and several microclimate attributes (AIRTEMP—air temperature, AIRHUMI—air humidity, SOILTEMP—soil temperature, SOILMOIST—soil moisture, DM—dry matter) on ant community structure in Mount Carmel, Israel. The eigenvalues of axis 1 (horizontally) and axis 2 (vertically) are 0.64 and 0.42, respectively; the eigenvalue of axis 3 (not displayed) is 0.25. Axes 1 and 2 explain 37% and 24% of the variance, respectively. Broken lines indicate three species groups (see text). Ant species (triangles) abbreviations: Aph sp.—*Aphaenogaster* sp. (Myrmicinae), Apespl—*Aphaenogaster splendida* (Myrmicinae), Camfel—*Camponotus fellah* (Formicinae), Camreb—*Camponotus rebecca* (Formicinae), Carbat—*Cardiocondyla batesi* (Myrmicinae), Careme—*Cardiocondyla emeryi* (Myrmicinae), Carmau—*Cardiocondyla nuda mauritanica* (Myrmicinae), Carnod—*Cataglyphis nodus* (Formicinae), Catnig—*Cataglyphis niger* (Formicinae), Cremos—*Crematogaster mosis* (Myrmicinae), Creeme—*Crematogaster emeryi* (Myrmicinae), Creion—*Crematogaster ionia* (Myrmicinae), Crejeh—*Crematogaster jehovae* (Myrmicinae), Crenig—*Crematogaster nigriceps* (Myrmicinae), Lasali—*Lasius alienus* (Formicinae), Lasbru—*Lasius brunneus* (Formicinae), Lepbip—*Lepisiota bipartita* (Formicinae), Lepspl—*Lepisiota splendens* (Formicinae), Lepsyr—*Lepisiota syriaca* (Formicinae), Leprec—*Leptothorax recedens* (Myrmicinae), Mesheb—*Messor hebraeus* (Myrmicinae), Monden—*Monomorium dentigerum* (Myrmicinae), Mongra—*Monomorium gracillimum* (Myrmicinae), Monnil—*Monomorium niloticum* (Myrmicinae), Monven—*Monomorium venustum* (Myrmicinae), Monsub—*Monomorium subopacum* (Myrmicinae), Myrgra—*Myrmecina graminicola* (Myrmicinae), Plaanc—*Plagiolepis ancyrensis* (Formicinae), Tapisr—*Tapinoma simrothi* (Dolichoderinae), Tapsim—*Tapinoma simrothi* (Dolichoderinae), Tetluc—*Tetramorium lucidulum* (Myrmicinae), Tetsah—*Tetramorium sahlbergi* (Myrmicinae), Tetsig—*Tetramorium signatum* (Myrmicinae), Tet sp.—*Tetramorium* sp. (Myrmicinae).

*halepensis* microhabitat, 23 species were sampled, with a Chao1 estimate of  $53.2 \pm 28.6$  species. Bonferroni post-hoc comparisons revealed significant differences ( $p < 0.05$ ) between each pair of microhabitats except between *Cistus* sp. and *Q. calliprinos*.

Ant community structure was analyzed by CCA and its ordination is shown in Fig. 4.

The horizontal axis was mainly affected by the various microhabitats, with a strong effect of *Q. calliprinos* (on the right side of the X-axis), a strong effect of *Cistus* sp. (on the left side of the X-axis), and a much lower effect of the other two microhabitats. The vertical axis was mainly related to microclimate conditions with a strong effect of air temperature, air humidity, and soil temperature, and a much lower effect of soil moisture and dry organic matter (on the upper part of the Y-axis). This axis was also related to *Pinus halepensis* and *Pistacia lentiscus* microhabitats (on the upper part of the Y-axis). The two axes accounted for 60.7% of the variance in the species-environment relation. Based on the CCA ordination we defined three distinct ant communities (Fig. 4): (1) the *Quercus calliprinos* community, comprised of northern origin species that are usually active during the cold and wet seasons; (2) the *Pinus halepensis*–*Pistacia lentiscus* community, comprised of spring-active species that mostly feed on honeydew; and (3) the *Cistus* community, comprised of summer-active species that feed mostly on honeydew.

## DISCUSSION

### Effect of fire and seasonality on ant community structure

Fire in the Aleppo pine forest on Mount Carmel had short- and medium-term positive effects on ant species richness. High species richness was observed at both the 1- and 14-year post-fire stands relative to the unburnt stand. A similar post-fire pattern was observed on Mount Carmel for plants (Arianoutsou and Ne'eman, 2000), granivorous birds (Izhaki and Adar, 1997; Izhaki, 2000) and mammals (Haim, 2000), as well as for ants in Australian ecosystems (Andersen, 1991; Parr et al., 2002; Hoffmann, 2003; Andersen et al., 2006). Fire has a marginal direct negative effect (e.g., mortality) on ants as they probably find refuge in their underground nests (Andersen and Yen, 1985). However, it appears that the indirect effects caused by fire on Mount Carmel within the first 14 years post-fire, including the modification of vegetation and the subsequent impact on abiotic factors and on food sources (New and Hanula, 1998), have a positive effect on ant species richness. Thus, the new environmental conditions in the burnt forest were favored by more ant species. This finding is in accordance with previous studies in fire-adapted habitats, where fire was shown to be beneficial for ants as it increases plant growth and seed production, mobilizes nutrients, and clears obstructions to foraging (e.g., Andersen and Yen, 1985; Andersen, 1988; Neumann, 1991, 1992; Jackson and Fox, 1996). Furthermore, fire intensity in a pine forest is not uniform and thus produces a patchy environment with high habitat complexity. As post-fire succession continues, we assume that the burnt forest becomes much more homogenous with regard to its biotic and abiotic conditions and thus less diverse in microhabitat availability. Hence, the 1- and 14-year post-fire stands were relatively heterogeneous in comparison to the unburnt stand and had greater species richness.

The ant community assemblage in the recently burnt forest differed strikingly from that in the unburnt forest, with only four shared ant species. This post-fire shift in community structure may represent the drastic post-fire changes in the biotic and abiotic

conditions. For example, *Pinus halepensis*, which burns completely during a fire, is essential for many ant species, either directly as their microhabitat or indirectly by harboring their food supply such as aphids (Soussan, 1990). The post-fire disappearance of trees and shrubs that blocked direct solar radiation on the surface before the onset of fire causes an increase in soil temperature and moisture (Dlusskii and Putyatina, 2004), and thus enables the inhabitation of thermophilic species. Furthermore, plants that characterize the first post-fire successional stages are those with massive seed production that enables the inhabitation of granivorous species. As the forest gradually recovers, plant cover and seed production increase for ca. 10–15 years and then decrease (Auld, 1995), with both trends forcing a change in ant species composition. Vegetation cover imposes changes on ant assemblage in other ecosystems (e.g., Arnan et al., 2006; Corley et al., 2006), as well as on the microhabitat scales investigated in our study (see below). However, it should be noted that our study does not demonstrate that fire is the direct causal factor of the differences detected in ant communities. Rather, chronosequence methodology enabled us to demonstrate indirectly the effect of fire on ant communities among the three observed forest stands.

Our cluster analysis enabled us to rank the impacts of season versus fire on the ant community structure on Mount Carmel. In particular, the differences in ant community assemblages that we found between the 1- and 14-year post-fire stands appear to be affected by season more than by the time that elapsed since a fire event. Conversely, the differences between the ant assemblages of the unburnt forest and the two burnt forests were mainly governed by the occurrence of fire rather than by season. In another study, Izhaki et al. (2003) also revealed a much stronger short-term impact of season than fire on ant community composition in a longleaf pine forest in Florida.

The changes in the proportion of ant species from different functional groups along post-fire succession provided important information on the origin of the differences in ant assemblages among the three forest stands. While the percentage of opportunistic species decreased with the time elapsed since a fire event, the proportion of generalist Myrmicinae showed an opposite trend. Thus, generalist Myrmicinae replaced the opportunists during the post-fire succession. A similar phenomenon was observed in progressive land abandonment in northern Mediterranean agroecosystems (Gómez et al., 2003) and in burnt and grazed habitats in Australia (Andersen, 1990). Indeed, the changes in these two functional groups were often correlated with the disturbance level (Andersen, 1990). Opportunists rapidly colonize disturbed habitats but are poor competitors and thus are characteristic of the early successional stages. Although generalist Myrmicinae are also unspecialized, they are highly competitive, especially in areas where the dominant Dolichoderinae are absent (e.g., Gómez et al., 2003), as in the case of Mount Carmel.

### **Effect of microhabitat on ant community structure**

A novel finding emerging from the current study is that the composition of the ant community in the mature Aleppo pine forest depends to a great extent on the plant species under which it dwells. Thus, the ground under the canopy of each plant species creates

a unique microhabitat with different biotic and abiotic factors, such as accumulated dry organic matter, soil moisture and temperature, and air temperature and humidity, all of which govern ant community composition. The environmental conditions under *Q. calliprinos* were unique, with high soil moisture, dry organic matter, and low soil temperature. Canonical Correspondence Analysis (CCA) revealed that the attributes of this microhabitat seem to be favored by several ant species such as *Aphenogaster splendida* (Myrmicinae) and *Cataglyphis nodus* (Formicinae). However, most ant species preferred high soil and air temperatures, high air humidity, and lower amounts of dry matter, which are characteristic features of the *Pinus halepensis* and *Pistacia lentiscus* microhabitats. It appears that the abiotic conditions had a stronger effect on the composition of ant communities beneath *Pinus halepensis* than beneath *Pistacia lentiscus*, as indicated by the differences in the length of their respective arrows in the CCA ordination. Furthermore, the *Pinus halepensis* microhabitat had the highest true ant species richness (Chao1 > 50), whereas the lowest true richness (Chao1 < 20) was detected beneath *Cistus*. Indeed, CCA showed that only a few species, such as *Monomorium niloticum* (Myrmicinae) and *Messor hebraeus* (Myrmicinae), favored the microhabitat conditions under *Cistus*.

Nevertheless, our CCA explained only 61% of the variance in the species-environment relation, with the remaining 39% possibly explained by factors that were not measured in this study. Plant structure, for example, affects the level of solar radiation that reaches the soil surface and thus governs local ant foraging and diversity (e.g., Whitford, 2009). Tree species commonly differ not only in their litter mass but also in their nitrogen content and mineralization rate, as well as in the acidity in the area under their influence (reviewed by Binkley and Giardina, 1998). Although we did not measure these variables, previous studies indicated that soil nutrient content affects ant community composition (Ellison et al., 2002). Furthermore, differences in the chemical composition of litter among plant species are likely to favor the occurrence of different types of fungi, bacteria, collembolans, and other invertebrates, all of which conceivably constitute part of the food web that is conducive to the diversity of ant species (Byrne, 1994; Kaspari, 1996). Hence, further study is needed to determine whether different microhabitat conditions beneath the canopies of different plant species promote differential ant communities.

## CONCLUSIONS

Because ants are tightly associated with soil and ground-level vegetation, they have proven to be valuable bioindicators in numerous biodiversity studies worldwide. Furthermore, responses of ants to disturbances mirror the responses of other arthropods (Majer, 1983). Anthropogenic activities are responsible for much of the decrease in biodiversity in Mediterranean ecosystems (Sala et al., 2000). Understanding the causes and consequences of ant diversity is critical to preserving both ecosystem functions and the services provided by ants (Folgarait, 1998). Our study points to the importance of seasonality in the Mediterranean ecosystem, which is probably correlated with resource

availability. Beyond the clear role of season, ants on Mount Carmel are also significantly affected by both macro- and micro-scale factors. Various combinations of these factors generate a complex and heterogeneous mosaic of habitat structures. This patchiness, evident on several simultaneous spatial and temporal scales, promotes a high species diversity of ants as well as of other organisms on Mount Carmel (e.g., Izhaki and Adar, 1997; Haim, 2000). Therefore, from the biodiversity restoration point of view, it is essential to adapt a management policy that is aimed at maintaining heterogeneity on both the macro-scale level (e.g., different fire regimes and post-fire management) and the micro-scale level (e.g., restoring the variety of plant species).

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