

# Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment

**Abstract** The present study analyzed ant community structure and the factors affecting it in the Spanish Mediterranean area. The aim of this study was to test whether temperature controls the composition and diversity of the ground ant fauna and the spatial and temporal distribution of dominance groups along adjacent communities. The main descriptors of community structure (except perhaps species richness) were found to vary along the gradient of vegetation cover: increased vegetation cover resulted in an increase in the relative abundance of the most common species, which led to a significant decrease in species evenness, together with a reduction in total ant density on the ground. In open habitats, dominant and subordinate species were abundant during different periods of the day, and this led to an increase in species evenness. In areas with high vegetation cover, dominants benefited from the lower temperatures by lengthening their periods of activity. This resulted in a decrease in the abundance of subordinate species, and in lower evenness. Seasonal patterns in community structure tracked temperature fluctuations and varied between habitat types. Evenness was similar in the two habitat types in spring, but increased in grasslands and decreased in shrublands/forests in summer. Species richness did not vary between seasons or habitat types. The relative abundance of dominance groups in the two types of habitats showed a different pattern between seasons. In grasslands, subordinates increased and dominants decreased their relative abundance from spring to summer, while in shrublands/forests, the opposite pattern was found. The overall conclusion from this study is that ground ant communities in open areas are primarily regu-

lated by temperature variations, while in shrublands and forests, dominant species are more abundant, and competitive interactions appear to be the major structuring force.

**Key words** Ant · Spatial variability · Temporal fluctuations · Vegetation cover · Diversity

## Introduction

Empirical evidence from natural communities suggests a causal relationship between diversity and productivity or heterogeneity of the system (Rosenzweig and Abramsky 1993; Putman 1994). In a number of studies (see review in Putman 1994), diversity has been demonstrated to be positively related to vegetative complexity, which effectively creates a wider potential diversity of available niches: the more complex an environment, the more finely its resources may be divided and thus the richer its fauna and flora (MacArthur 1972). Nevertheless, other models of the control of diversity within communities suggest that there is a humped relationship between local species diversity and the gradient of productivity: diversity rises over low productivities and falls over high productivities (Grime 1979; Rosenzweig and Abramsky 1993). With high productivity, a few species can attain competitive dominance and exclude other species, whereas at low productivity, only a few stress-tolerant or generalist species can survive (Bestelmeyer and Wiens 1996). In ants, there is considerable evidence that interspecific competition contributes to patterns of distribution and abundance of species and communities (Andersen 1992; Human and Gordon 1996; Morrison 1996). Hölldobler and Wilson (1990) have proposed “the dominance-impoverishment rule”, which states that an inverse relationship exists between species richness and the degree of competitive dominance in ant communities, i.e. the fewer the ant species in a local community, the more likely the community is to be dominated behaviourally by one or a few dominant species. Nevertheless,

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J. Retana (✉)  
Unidad de Ecología y CREAM, Facultad de Ciencias,  
Universidad Autónoma de Barcelona,  
08193 Bellaterra (Barcelona), Spain  
e-mail: retana@cc.uab.es  
Tel.: +34-93581-2028, Fax: +1-34-93581-1312

X. Cerdá  
Unidad de Ecología Evolutiva, Estación Biológica de Doñana,  
CSIC, Apdo. 1056, 41080 Sevilla, Spain

other studies directly contradict Hölldobler and Wilson's rule, and show that the richness and diversity of ant species exhibit humped patterns in relation to gradients of stress and dominance (Andersen 1992, 1997; Morrison 1996). When the number of dominant ants is low, so is species diversity. At these times, environmental conditions are generally unfavourable for ants. As environmental conditions improve, so does total species diversity (Majer 1985; Gallé 1991; Andersen 1992; Perfecto and Snelling 1995; Perfecto and Vandermeer 1996). The abundance of dominant species also increases with favourable conditions, and leads to a decrease in species diversity, presumably because of competitive exclusion (Andersen 1992).

However, variation in both time and space is a striking feature of many real communities (Chesson 1986). Stochastic environments can lead to coexistence: competing species that cannot coexist in a constant environment may be able to coexist in the presence of environmental variation (Kareiva 1989). Many aspects of the climate fluctuate in a regular and predictable way. If this temporal variability is such that different species are abundant at different times, then abundance will be averaged out in the long term and diversity will increase (Yodzis 1986). The combination of temperature and humidity can be used to define climates favorable for ant activity (Hölldobler and Wilson 1990). Areas that are exposed to wind and direct sunlight are drier and warmer than those that are protected by a canopy cover. Thus, variations in vegetative structure may either enhance or reduce ant diversity by increasing or reducing habitat heterogeneity, microclimate suitability or the activity of dominant species, depending on the proportion of the regional ant fauna that is composed by cold- or heat-adapted taxa. In some ant communities, these variations in canopy cover do not differentially affect the activity of dominant species compared to other species, because the foraging activity in relation to temperature of dominant and other ant species is similar (Andersen 1992; Human and Gordon 1996). Nevertheless, in Mediterranean communities, the foraging requirements of dominant species are not typical of other ants: dominants are heat-intolerant species that are restricted largely by physical conditions, while subordinates are heat-tolerant species that are active over a wider range of temperatures (Cerdá et al. 1997, 1998a, 1998b). In these Mediterranean areas, the limited thermal tolerance of dominant species compared with that of subordinates may disrupt the expected transitive hierarchies, and allow subordinates to be abundant in certain seasons and habitats (Cerdá et al. 1997; Cros et al. 1997).

What forces serve to organize ant communities in each situation, and how are they put into action? Temperature stress has been highlighted as the principal abiotic stress regulating ant community structure in Australia (Andersen 1995), because low temperatures limit the abundance of dominant ants, and therefore largely determine competitive dynamics within the community. The aim of this study was to test whether temperature (in this

case, high temperatures) controls the composition and diversity of the ground ant fauna and the spatial and temporal distribution of dominance groups along adjacent communities in the Mediterranean area. The questions addressed in this study were: (1) does variation in temperature determine spatial and temporal variations in the structure of Mediterranean ground ant communities? and (2) how does the different response to temperature by dominance groups contribute to changes in community structure?

## Materials and methods

### Study sites

The study was performed in 17 sites over eight locations distributed from north-eastern to southern Spain (Table 1). We selected sites that encompassed a considerable variety of vegetation cover. Vegetation cover was determined in each site as the percentage of the total ground surface that was in the shade of trees, shrubs or large herbs (i.e. not exposed to the sun) at midday on clear summer days. This percentage was estimated by monitoring 100–200 randomly distributed points in each site and determining whether they were in the sun or in the shade. In the study sites, vegetation cover ranged from 5 to 90% (Table 1).

### Sampling

Pitfall traps were used to measure ground ant abundance of each site. They provide a good estimate of the relative abundances of ant species foraging on the ground (Romero and Jaffe 1989; Olson 1991; Klimetzek and Pelz 1992; Andersen 1997), but probably undersample the complete ant community, especially arboreal-nesting ants (Marsh 1984; Majer 1997). Variation in temperature within Mediterranean ecosystems shows marked differences between seasons. This led us to distinguish two contrasting periods within the usual activity period of most species (from early spring to mid-autumn, with a peak in mid-summer; see Cros et al. 1997): a cool period in spring or autumn and a hot period in summer. Traps were laid during these two different periods: sampling was conducted in mid-May (spring period) and repeated in mid-July (summer period), except in the Boalar de Jaca sites, which were sampled only once. In each sampling period, traps were operated for 4–6 days. Similar trap numbers were used at each site: four or five series of five traps (with 5-m spacing between traps and variable spacing between series) were laid over the study area. Pitfall traps were 6-cm-diameter, 7-cm-deep plastic vials partially filled with water, ethanol and soap. Ants were sorted in the laboratory to the species level (see species list in the Appendix).

Baits were used to quantify the relationship between temperature and external activity of each species, and the behavioural dominance of species at food resources. In sites where baits were not placed (sites 4, 5, 6, 11, 12 and 13; Table 1), we used information already collected in other studies in the same way. In the Portbou, Boalar de Jaca and Sierra Sur sites (sites 7–10 and 14–17), four series of five baits were laid randomly over the entire study area for a total of four sampling days of 24 h each in mid-May, and repeated in mid-July (except in the Boalar de Jaca sites, which were only sampled in May). The three Canet de Mar sites (sites 1–3) were also used for another study (Cerdá et al. 1997), and were sampled more intensely: five series of six baits were placed for a total of 6 days in spring and 6 days in summer. The same type of bait was used at all sites. They were plastic discs with different large food rewards (honey, bacon, sausage, cheese and biscuit) that were attractive to ants. These baits could not be transported to the nest by individual workers. Each hour of each 24-h sampling period, the number of ants of each species feeding at each bait and the interactions among species were noted. Three

**Table 1** Summary descriptions of the study sites, distributed from north-eastern to southern Spain

Site number	Location	Grid reference	Vegetation type	Vegetation cover (%)	Sampling area (m <sup>2</sup> )
1	Canet de Mar (Barcelona)	41°25' N 2°37' E	Grassland	25	2000
2	Canet de Mar (Barcelona)	41°25' N 2°37' E	Open holm oak forest	40	1100
3	Canet de Mar (Barcelona)	41°25' N 2°37' E	Open pine forest	60	1500
4	Serra de l'Obac (Barcelona)	41°37' N 2°7' E	Forest gap	60	600
5	Serra de l'Obac (Barcelona)	41° 37' N 2° 07' E	Open holm oak forest	70	600
6	Serra de l'Obac (Barcelona)	41°37' N 2°7' E	Holm oak forest	90	600
7	Portbou (Gerona)	42°26' N 3°26' E	Grassland	20	1000
8	Portbou (Gerona)	42°26' N 3°26' E	Shrubland	40	1000
9	Portbou (Gerona)	42°26' N 3°26' E	Open mixed forest	40	1500
10	Sierra Sur (Jaén)	37°40' N 3°41' W	Grassland	5	2500
11	Doñana National Park (Huelva)	37°1' N 6°33' W	Grassland	10	2000
12	Bellaterra (Barcelona)	41°21' N 2°3' E	Grassland	25	3000
13	Serra de Collcerola (Barcelona)	41°24' N 2°8' E	Shrubland	60	1500
14	Boalar de Jaca (Huesca)	42°8' N 0°30' W	Grassland	10	1000
15	Boalar de Jaca (Huesca)	42°8' N 0°30' W	Grassland-shrubland	25	800
16	Boalar de Jaca (Huesca)	42°8' N 0°30' W	Forest gap	40	600
17	Boalar de Jaca (Huesca)	42°8' N 0°30' W	Oak forest	70	1000

different types of interspecific interactions were distinguished: (1) expulsion; one species driving another away and occupying the bait; (2) escape, of the expelled species from the bait following attack by another; (3) coexistence of different species at the same bait in the same sampling period. Ground surface temperatures in the sun and the shade were measured in each site with a digital thermometer, together with the hourly measurements at baits.

#### Data analysis

To describe the structure of each ant community, the two components of species diversity, species richness ( $S$ ) and evenness, were estimated for each site (data from spring and summer periods pooled together) and for each sampling period considered separately. Two indexes of evenness were calculated.

(1) The evenness index of Pielou ( $J$ ) was estimated as:

$$J=H/\ln S$$

where  $S$  is species richness and  $H$  is the Shannon index of diversity:

$$H=-\sum(p_i \ln p_i)$$

where  $p_i$  is the proportion of workers of the  $i$ th species in traps during the period of time considered.

(2) Since various authors (Alatalo 1981; Lande 1996) have criticized the  $J$  index because it is strongly affected by species richness, another measure of evenness relatively unaffected by species richness, the modified Hill's ratio ( $F$ ), was also calculated:

$$F=[(1/\sum(p_i^2))-1]/(e^H-1)$$

In addition, we also calculated an abundance index that expresses the abundance of the most common species (one, two, or three) as a fraction of the total number of individuals collected in traps, and is a measure of numerical dominance.

Behavioural dominance of ant species was determined by observing interspecific interactions at baits (data from spring and summer periods pooled together). For each species, we calculated the dominance index [sensu Fellers (1987) or Cerdá et al. (1997, 1998b)], which was the percentage of encounters won (i.e. the species drove away another species) in all of its interspecific encounters. A dominance hierarchy was established according to

this index (Cerdá et al. 1997, 1998a, 1998b). From the position of each ant species in the dominance hierarchy, we classified it into one of two behavioural groups: (1) dominants, which were at the top of the dominance/aggressiveness hierarchy, and drove away the majority of ant species from food resources; (2) subordinates, which were at the bottom of the dominance/aggressiveness hierarchy, and were forced to abandon the baits by dominants. Cut-off points for distinguishing dominants from subordinates were established in each community according to two criteria: dominant species were those that (1) had a dominance index greater than 50%, or (2) had a dominance index which did not statistically differ (based on a  $\chi^2$ -test) from that of species classified as dominants following the first criterion. Since we did not have our own data for species from all communities studied, we used unpublished information provided by various colleagues (Sebastiá Cros, Soledad Carpintero, Anna Alsina) to assign species from Bellaterra, Collcerola, Doñana and Serra de l'Obac sites to these behavioural categories.

In the analyses of differences between seasons, sites with a vegetation cover less than 30% were considered grasslands, while those with a vegetation cover greater than 30% were considered shrublands/forests. Thus, five grassland replicates and eight shrubland/forest replicates were used, because the Boalar de Jaca sites were only sampled in spring and not included in these analyses. The effects of habitat type (grassland versus forest) and season (spring versus summer) on richness, evenness and mean number of ants per trap were tested by two-way ANOVAs. Data were log or arcsine square root transformed when necessary.

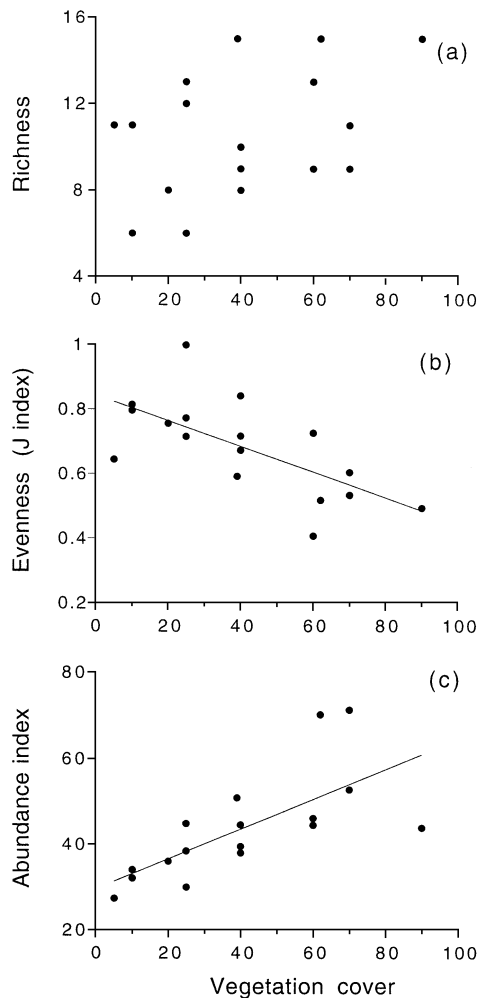
## Results

### Spatial variation: effect of vegetation cover on community structure

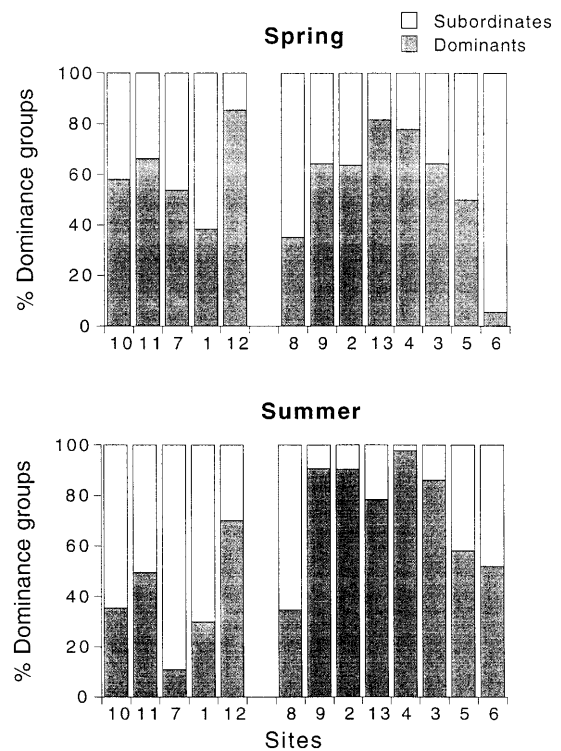
A linear regression did not show a significant relationship between vegetation cover (i.e. the percentage of shade at midday on summer days) and species richness ( $P=0.16$ ,  $n=17$ ). However, both indexes of evenness decreased with canopy cover: the  $J$  index ( $R^2=0.44$ ,  $P=0.004$ ,  $n=17$ ) (Fig. 1) and the modified Hill's ratio ( $R^2=0.31$ ,  $P=0.018$ ,  $n=17$ ). The relative abundance of the most common species in traps showed a significant posi-

**Table 2** Mean ( $\pm$ SE) values of different thermal features of the sites where temperatures were registered hourly in the spring and summer periods. Spring and summer data have been compared using Mann-Whitney *U*-test (NS, not significant; \* $P < 0.05$ ; \*\* $P < 0.01$ ). The total number of sampling days was six (in both spring and summer) for sites 1–3, and four for sites 7–10

Site	Mean diurnal sun temperature		Midday sun temperature		Difference (sun temperature–shade temperature) at midday	
	Spring	Summer	Spring	Summer	Spring	Summer
<b>Grasslands</b>						
1	31.5 $\pm$ 2.4	41.2 $\pm$ 1.1**	41.6 $\pm$ 2.5	53.2 $\pm$ 1.5**	20.2 $\pm$ 1.5	23.2 $\pm$ 1.3 NS
7	31.7 $\pm$ 1.8	41.7 $\pm$ 1.1*	43.1 $\pm$ 2.1	52.0 $\pm$ 1.6*	20.4 $\pm$ 1.2	21.4 $\pm$ 0.6 NS
10	22.6 $\pm$ 0.7	37.8 $\pm$ 1.4*	33.8 $\pm$ 0.6	47.6 $\pm$ 1.5*	17.9 $\pm$ 0.2	19.6 $\pm$ 0.6*
<b>Forests/shrublands</b>						
2	32.1 $\pm$ 2.4	42.1 $\pm$ 1.9*	42.4 $\pm$ 2.8*	54.1 $\pm$ 2.2	21.0 $\pm$ 1.3	25.4 $\pm$ 1.6 NS
3	30.5 $\pm$ 3.0	44.9 $\pm$ 1.5**	40.6 $\pm$ 3.5	56.3 $\pm$ 1.8**	21.0 $\pm$ 0.6	27.4 $\pm$ 1.1**
8	31.3 $\pm$ 1.6	40.2 $\pm$ 0.8*	41.6 $\pm$ 1.8*	51.6 $\pm$ 1.7	20.1 $\pm$ 0.8	23.1 $\pm$ 1.0 NS
9	31.7 $\pm$ 1.3	40.1 $\pm$ 1.7*	42.3 $\pm$ 1.4	51.3 $\pm$ 1.7*	22.3 $\pm$ 1.9	22.9 $\pm$ 0.7 NS



**Fig. 1** Relationship between vegetation cover (i.e. the percentage of shade) and richness (a), evenness (*J* index) (b) and the abundance index (which expresses the abundance of the most common species as a fraction of the total number of individuals) (c) of ant species in pitfall traps ( $n=17$ )



**Fig. 2** Relative abundance of dominants and subordinates among all ants sampled in spring (a) and summer (b) in grassland and forest/shrubland sites along the vegetation cover gradient. Sites 14–17 have not been included because they were only sampled in spring

tive relationship with vegetation cover ( $R^2=0.49$ ,  $P=0.002$ ,  $n=17$ ), and the same trend was found when the abundance of the two or three most common species was used. Although we did not register absolute values of ant density on the ground in the different sites, data from traps indicated that total ant abundance was also lower in covered sites: the total number of ants collected per trap and per day (the two seasons pooled, data log transformed) was negatively correlated with canopy cover ( $R^2=0.47$ ,  $P=0.002$ ,  $n=17$ ).



## Temporal variation: seasonal patterns in community structure and temperature

There were no differences in richness and evenness (only the results concerning the  $J$  index are shown here, but those of  $F$  were similar) between seasons or between types of habitats ( $F_{1,22}<1.5$ ,  $P>0.10$  in all cases). The interaction between both factors was significant for  $J$  ( $F_{1,22}=5.8$ ,  $P=0.025$ ). On average,  $J$  was similar in the two habitat types in spring, but increased in grasslands and decreased in shrublands/forests in summer. The mean number of workers per trap (log transformed) was significantly different according to habitat type (two-way ANOVA,  $F_{1,22}=9.2$ ,  $P=0.006$ ), with grasslands having more workers per trap than shrublands/forests (mean $\pm$ SE: 16.8 $\pm$ 8.2 and 3.6 $\pm$ 0.8 workers per trap, respectively). This variable also varied with season ( $F_{1,22}=16.9$ ,  $P=0.0005$ ): the mean number of workers per trap was higher in summer than in spring (12.3 $\pm$ 5.3 and 4.9 $\pm$ 1.9 workers per trap, respectively). The interaction between the two factors was not significant ( $F_{1,22}=0.1$ ,  $P=0.81$ ).

Mean diurnal temperatures in the sun were significantly higher in summer than in spring in both grasslands and forests (Table 2), and the maximum ground sun temperature was reached in summer (frequently exceeding 50°C; value in spring around 40°C). Soil surface temperatures in full sun at midday were, in all types of habitats, 20–25°C greater than in the shade of the canopy in both spring and summer (Table 2).

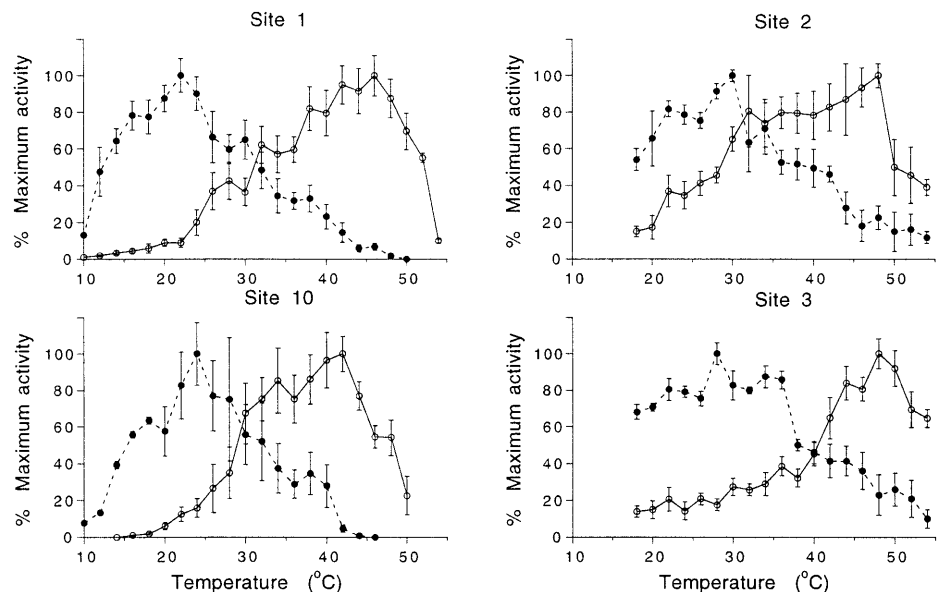
## Effect of temperature on dominance

Total abundance (i.e. number of ants per trap, log transformed) of both dominants and subordinates did not vary between seasons ( $F_{1,22}=4.2$ ,  $P=0.055$  for dominants;

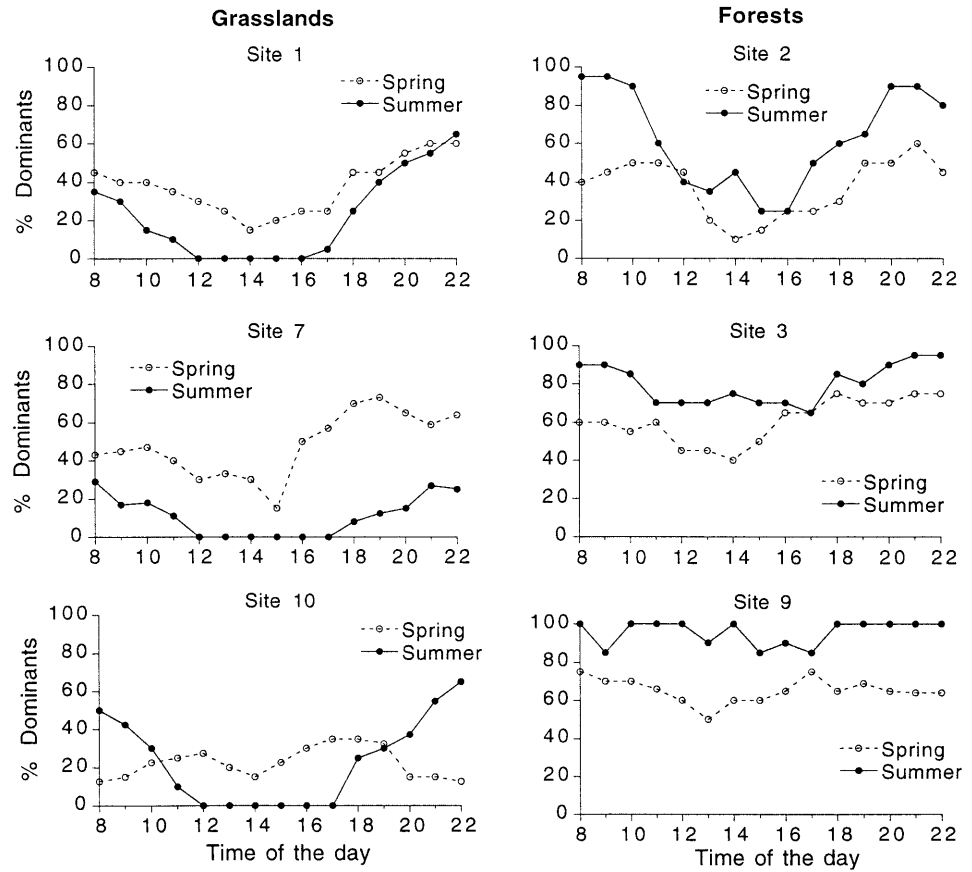
$F_{1,22}=1.3$ ,  $P=0.26$  for subordinates), but differed between types of habitats ( $F_{1,22}=7.6$ ,  $P=0.011$  for dominants;  $F_{1,22}=8.6$ ,  $P=0.008$  for subordinates), being larger in grasslands than in forests. The interactions between the two factors were not significant in either case ( $F_{1,22}=0.8$ ,  $P=0.38$  for dominants;  $F_{1,22}=1.2$ ,  $P=0.28$  for subordinates). The relative abundance of the two dominance groups (arcsine square root transformed) did not vary between seasons ( $F_{1,22}=0.03$ ,  $P=0.87$ ) or between types of habitats ( $F_{1,22}=2.6$ ,  $P=0.12$ ), but the interaction between the two factors was significant ( $F_{1,22}=4.7$ ,  $P=0.04$ ). On average, dominants comprised 60.4% of all ants at grassland sites in spring, but only 39.2% in summer. However, this pattern changed in forest/shrubland sites, where dominants accounted for 55.3% of ants in spring and 73.5% in summer. Comparisons between seasons in each site showed that the relative abundance of dominants decreased from spring to summer in all grassland sites ( $\chi^2$ ,  $P<0.05$ ; Fig. 2), while it increased from spring to summer in five out of eight forest/shrubland sites.

This decrease in dominants and the consequent increase in subordinates in summer in open sites could be related to the higher temperatures during this season (see Table 2). Dominants had their maximum activity at 20–30°C, but considerably diminished their activity at temperatures over 30°C (Fig. 3), which were frequently surpassed in summer. On the other hand, subordinates increased their activity at temperatures over 30°C, and reached their maximum activity at 40–50°C (Fig. 3). However, in covered sites, most of the ground surface was in the shade, where temperatures very seldom reached 30°C. Thus, dominants, which drastically reduced their summer foraging activity during the day in grassland sites, were less or not at all affected in forest sites (Fig. 4). This trend towards a greater presence of dominants in covered sites was also evident when the percentage of dominants (the two sampling seasons

**Fig. 3** Relationship between ground surface temperature (°C) and percentage of maximum activity of the two dominance groups (subordinates, open circles and unbroken line; dominants, closed circles and broken line; all species from the same group considered together) in two representative grasslands (sites 1 and 10) and two representative forests (sites 2 and 3). Each point represents the mean ( $\pm$ SE) activity value of all cases at the same temperature (in 2°C classes) from all hours of all sampling days in each site. Data for the two dominance groups have been standardized by defining the maximum mean activity value observed as 100% of activity



**Fig. 4** Daily variations on sunny days in the percentage of dominants at baits in spring (open circles and broken line) and summer (closed circles and unbroken line) in three grass-land (1, 7, and 10) and three forest (2, 3, and 9) sites



pooled) was regressed on the canopy cover of each site ( $R^2=0.33$ ,  $P=0.017$ ,  $n=17$ ).

## Discussion

Vegetation cover, through the percentage of shade created by the canopy, has proved to be a good predictor of the structure of the Mediterranean ground ant communities studied. The main descriptors of community structure (except species richness, which is a difficult variable to estimate, and is usually underestimated in field data; Lande 1996) were strongly related to vegetation cover (Fig. 1), despite the fact that each community was composed by a taxonomically distinct set of species (see the Appendix): increasing vegetation cover resulted in a progressive increase in the relative abundance of the most common species, which led to a significant decrease in species evenness, together with a reduction in total ant density on the ground. This pattern differs from that found in other ecosystems, where increasing complexity and canopy cover may lead to high diversity and reduced dominance in ants (Room 1975; Risch and Carroll 1982; Majer 1985; Gallé 1991; MacKay et al. 1991; Perfecto and Snelling 1995; Perfecto and Vandermeer 1996), or to humped distributions, because ant species diversity increases along the successional gradient until the communities become dominated by some dominant species, af-

ter which diversity declines (Majer 1985; Andersen 1992; Morrison 1996).

Although for some groups of animals, species richness and evenness might increase with structural complexity, which effectively creates a wider potential diversity of available niches (Putman 1994), a more structured and complex habitat will not necessarily provide the best environmental conditions for all groups of organisms. In some situations, greater complexity may negatively affect certain factors that might be important for allowing species' coexistence. This might be the case with temperature in Mediterranean environments. A high canopy cover implies a low percentage of ground surface exposed to the sun, and vice versa. Since the temperature in shaded areas remains considerably lower than in sunny areas (see Table 2), canopy cover determines the proportion of the ground surface subjected to low or high temperatures. In open habitats, such as the grasslands in this study, much of the ground surface is exposed to solar radiation, and this allows the daily range of temperature to be sufficiently wide to permit subordinate species to be active during the day, while dominants, which have a lower thermal tolerance (see Fig. 3), are restricted to dusk and night periods. The overall result on a whole-day basis is that there are several abundant ant species in different periods of the day, leading to an increase in species diversity. On the other hand, areas with greater vegetation cover are exposed to shade temperatures, i.e.

temperatures which fluctuate in a smaller range of variation, over a greater proportion of their ground surface. In these thermal environments, dominant, heat-intolerant species benefit from this attenuation by lengthening their periods of activity to times of the day in which temperatures reach critical values in open sites (Cros et al. 1997). The result at the community level is a decrease in the abundance of subordinate species (see Fig. 2), and a lower evenness of the ant fauna (see Fig. 1).

To this spatial variation is added temporal variation, because both mean and maximum ground temperatures are higher in summer than in spring (Table 2). In open sites, evenness is higher in summer than in spring, while dominants decrease and subordinates increase their relative abundance from spring to summer (Fig. 2). These changes are caused by the fact that summer temperatures are much higher than those in the spring, enabling subordinate species to be abundant during the middle of the day, while dominants are active at night. In forests, there is also a temperature increase in summer, but most of the ground surface is in the shade, where temperatures very seldom reach 30°C. This allows dominants to be active throughout the day (Fig. 4), and reduces species evenness.

A wider thermal range may increase species evenness because different species are favoured by different sorts of thermal conditions, such that gradual changes in the environment alter the competitive rankings of the species (Giller 1984). In tropical and boreal areas, the foraging activity in relation to temperature of dominants and subordinates is similar (Andersen 1992). Thus, dominant species may dominate all kinds of habitats, both open and shaded (Samways 1990). But in the Mediterranean communities studied, dominants forage at low temperatures (maximum activity at 20–30°C; see Fig. 3), quite distant from their critical thermal limits, while subordinates forage at high temperatures (maximum activity at 40–50°C), very close to their physiological thermal limits (Cerdá and Retana 1997; Cerdá et al. 1998a). Several studies have documented similar restrictions of aggressive species by physical factors, and wider physical tol-

erance for subordinate species (Brian 1955, 1956; Fellers 1989). In these ecosystems, long-term stability depends on short-term instabilities (Chesson and Huntly 1989): temporal changes in the foraging abundance of dominant species and in the order of competitive superiority among the species lead to an increase in the number of abundant species and, consequently, species evenness (Andersen 1992; Cerdá et al. 1997).

For small-bodied ectotherms such as ants, temperatures outside the range 10–45°C may be considered stressful, because they often approach or go beyond the critical thermal limits of many ant species (Hölldobler and Wilson 1990; Bestelmeyer 1997; Cerdá et al. 1997). Low temperatures determine competitive dynamics within the community in Australia and the USA, because the reduction in temperature caused by vegetation cover reduces the abundance of dominants (Andersen 1992, 1997). In Mediterranean areas [and also steppes and deserts; see Baroni Urbani and Aktaş (1981) or Heatwole and Muir (1989)], temperature (in this case, high temperatures) also controls the composition and structure of ground ant communities. Dominant ants in the competitive hierarchy are heat intolerant, and their external activity is limited by high temperatures. In open habitats, ant communities show few effects of biotic interactions and are primarily ordered by thermal variations. When habitat complexity increases, there is a lower thermal variation, dominant species become more abundant, and interspecific interactions, mainly competition, become the major structuring force for the ground ant fauna.

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**Appendix** List of ant species collected in pitfall traps in each sampling site

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<b>Myrmicinae</b>																	
<i>Aphaenogaster gibbosa</i>				X										X	X	X	X
<i>Aphaenogaster senilis</i>	X	X	X							X	X	X	X				
<i>Aphaenogaster subterranea</i>				X	X												
<i>Crematogaster auberti</i>							X	X									
<i>Crematogaster scutellaris</i>		X	X													X	
<i>Crematogaster sordidula</i>								X	X	X							
<i>Lasius alienus</i>	X																
<i>Lasius mixtus</i>						X											
<i>Lasius myops</i>				X	X	X											
<i>Leptothorax grouvellei</i>														X			
<i>Leptothorax krausei</i>				X	X	X											
<i>Leptothorax niger</i>	X											X					
<i>Leptothorax parvulus</i>																X	X
<i>Leptothorax recedens</i>		X	X														
<i>Leptothorax specularis</i>							X	X	X								
<i>Leptothorax tristis</i>																	X
<i>Leptothorax unifasciatus</i>				X	X	X											
<i>Messor barbarus</i>										X		X					
<i>Messor bouvieri</i>	X		X									X	X				
<i>Messor capitatus</i>	X	X	X				X	X	X			X	X				
<i>Messor lusitanicus</i>											X						
<i>Myrmica sabuleti</i>					X	X								X		X	X
<i>Myrmecina graminicola</i>					X												
<i>Pheidole pallidula</i>	X	X	X	X		X		X	X	X		X	X			X	X
<i>Tetramorium caespitum</i>				X											X	X	
<i>Tetramorium hispanicum</i>											X						
<i>Tetramorium semilaeve</i>	X	X	X				X	X	X	X		X	X				
<b>Formicinae</b>																	
<i>Camponotus aethiops</i>														X		X	X
<i>Camponotus cruentatus</i>		X	X	X	X	X				X			X				
<i>Camponotus foreli</i>	X	X	X									X					
<i>Camponotus piceus</i>				X	X	X		X		X				X			
<i>Camponotus pilicornis</i>		X	X	X	X	X											
<i>Camponotus sylvaticus</i>	X	X	X				X	X	X			X	X				
<i>Camponotus truncatus</i>				X		X											
<i>Cataglyphis cursor</i>	X	X	X														
<i>Cataglyphis iberica</i>												X					
<i>Cataglyphis floricola</i>											X						
<i>Cataglyphis rosenhaueri</i>										X							
<i>Cataglyphis velox</i>										X							
<i>Diplorhoptrum</i> sp.	X	X	X				X	X	X								
<i>Formica cunicularia</i>															X		
<i>Formica gagates</i>				X	X	X								X		X	X
<i>Formica gerardi</i>				X	X	X											
<i>Formica rufibarbis</i>														X			
<i>Formica subrufa</i>				X			X				X						
<i>Plagiolepis pygmaea</i>	X	X	X	X		X	X	X	X	X		X	X	X	X	X	X
<i>Proformica nasuta</i>												X					
<b>Dolichoderinae</b>																	
<i>Linepithema humile</i>											X						
<i>Tapinoma erraticum</i>														X	X	X	X
<i>Tapinoma nigerrimum</i>	X	X	X							X		X	X	X	X		

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