

Vegetation cover and elevation drive diversity and composition of ant communities (Hymenoptera: Formicidae) in a Mediterranean ecosystem

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Abstract

Identifying the environmental parameters governing patterns of biodiversity and community composition is particularly important for planning conservation schemes and predicting response of communities to global change. To highlight the parameters most relevant for explaining patterns in ant assemblages at a local scale, we described ant communities in 95 plots distributed along environmental gradients on a mountain in the Mediterranean region of southern France. Among the six environmental parameters considered (slope, exposition, elevation, tree basal area, tree species diversity, and the dominant tree species), tree basal area (a good proxy for tree cover) and elevation had by far the strongest influence on ant species richness, diversity, and community composition. Ant richness and diversity decreased with increasing tree cover and elevation. Tree cover had a stronger effect than elevation, corroborating the longstanding hypothesis that radiant energy that heats foraging substrates might be more relevant to ants than average temperature. Deciphering local processes that structure communities contributes to a better understanding of global patterns.

Key words: Community ecology, environment, elevation, gradient, Formicidae.

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Introduction

Identifying the environmental parameters that govern species distributions and the composition of communities at local and global scales is key to understanding ecosystem dynamics and spatial patterns of biodiversity. For instance, knowing these parameters is particularly useful for predicting responses of species and ecosystems to ongoing climate change and for treating other questions in biodiversity conservation (e.g., HODKINSON 2005, GUÉNARD & al. 2012). Ecologists have long documented global patterns of biodiversity along latitudinal or elevational gradients but the underlying mechanisms are still debated (GASTON 2000, WILLIG & al. 2003, CURRIE & al. 2004). Although some universal patterns are undisputed – decrease of diversity with increasing elevation and latitude – the response to environmental parameters varies across taxonomic groups (MCCAIN & GRYTNES 2010). This must be taken into consideration for a more accurate understanding of ecosystem composition and dynamics.

The case of ants, compared with other insects, is particularly illustrative of variation across taxa in response to

environmental gradients. Apart from rare cases showing no relationship between ant diversity and elevation (e.g., ORABI & al. 2011), ant diversity is shown to decrease with increasing elevation following three types of relationships: linear decrease (ARAÚJO & FERNANDES 2003, HAGVAR 2005, GLASER 2006, LESSARD & al. 2007), exponential decrease (BRÜHL & al. 1999), and mid-elevation peak (SAMSON & al. 1997, FISHER 1998, VAN DER HAMMEN & WARD 2005, SABU & al. 2008, LONGINO & COLWELL 2011, DEL TORO 2013, SMITH & al. 2014). In the tropics, the drop of ant diversity toward the top of altitudinal gradients can be particularly strong – whatever the shape of the relationship – (e.g., JANZEN 1973, SAMSON & al. 1997, BRÜHL & al. 1999, LONGINO & COLWELL 2011) when compared with the diversity of other insects, such as flies (Diptera) (JANZEN & al. 1976). Interestingly, as noted by JANZEN (1973), this drop is also less pronounced in temperate-climate regions, except for particularly humid areas such as wet coastal mountain ranges. This difference between ants and flies and between tropical and temperate

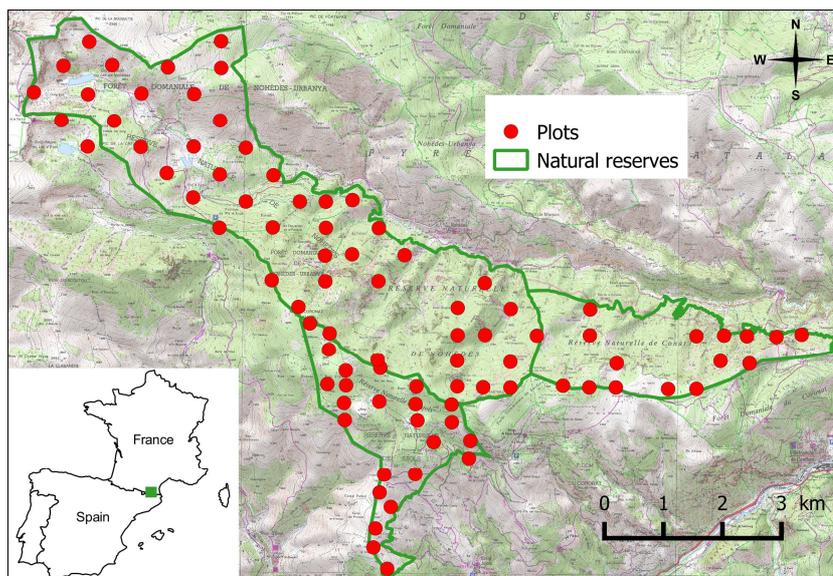


Fig. 1: Localisation of the study site and sampling plots. Delimitation of the natural reserves of Nohèdes (North), Conat (East), and Jujols (South) is given.

environments for ants can be explained by the hypothesis that radiant energy is the most limiting factor for ants and that humidity and cloud cover, which are particularly important on tropical mountains, dissipate radiant heat (JANZEN 1973, 1983, OLSON 1994, FISHER 1996). Thus, the linear decrease of average temperature with increasing elevation is not the only parameter driving ant diversity. Similarly, average temperature does not fully explain global patterns in the distribution of ant diversity (JENKINS & al. 2011). Although recently developed macro-ecological approaches are greatly contributing to the understanding of ant diversity patterns at the global scale (KASPARI & al. 2004, DUNN & al. 2007, SANDERS & al. 2007, DUNN & al. 2009a, b, GUÉNARD & al. 2012, ECONOMO & al. 2015), we still need investigations at a local scale to dissect mechanisms underlying diversity patterns.

The relatively large body of literature on the response of ants to environmental gradients in lowland Mediterranean landscapes provides details about the mechanisms driving responses of ant communities to temperature. A first point is that open habitats may support communities that have higher evenness (i.e., species have closer relative proportions) than forested habitats because they experience stronger daily and seasonal variation of temperature, especially at ground level. This variation allows coexistence of heat-tolerant subordinate and heat-intolerant dominant species through temporal variation of foraging activity patterns (CERDÁ & al. 1997, CROS & al. 1997, CERDÁ & al. 1998a, CERDÁ & al. 1998b, RETANA & CERDÁ 2000). A second point is the finding that functional traits in Mediterranean ant communities vary along environmental gradients and are strongly influenced by temperature, precipitation and tree cover (ARNAN & al. 2012, BERNADOU & al. 2013). It has also been shown that the degree of habitat openness affects ant community composition (MUNYAI & FOORD 2012, BERNADOU & al. 2013), and is positively correlated with ant diversity (ARNAN & al. 2009, DEL TORO 2013, DEL TORO & al. 2013, BERNADOU & al. 2015) and evenness (RETANA & CERDÁ 2000). Although it is acknowledged that elevation, temperature and vegetation cover influence patterns of ant communities and diversity, a causal link between vegetation cover and ant diversity due to

the effect of cover on the amount of radiant energy that heats foraging substrates has never been explicitly tested.

We took advantage of a thorough survey of the ants of Mount Coronat (LEBAS & al. 2015), in southern France, to investigate the relative importance of various abiotic parameters in explaining ant diversity and community composition and to propose a direct link between these parameters and the radiant-energy hypothesis, i.e., the hypothesis that radiant energy that heats foraging substrates is among the factors most constraining ant diversity and community composition. The ant survey was performed on plots where vegetation parameters had also been recorded, allowing testing for relationships between vegetation and the diversity and composition of ant communities.

Material and methods

The study area consisted in three contiguous natural reserves (Conat, Jujols and Nohèdes) covering a total of 3158 ha on the eastern, northern and southern slopes of Mount Coronat, located at the eastern end of the Pyrenees mountain chain in southern France. The area is 60 km from the Mediterranean Sea and elevation ranges from 600 to 2460 m above sea level (a.s.l.). As a consequence, it displays a strong environmental gradient from a Mediterranean climate with dry summers and cold humid winters to a wet mountain climate. The village of Nohèdes (N42.62283, E2.28917, 970 m a.s.l.), located on the edge of the natural reserve, 3 km away from the top of mount Coronat, experiences monthly mean minimum and maximum temperatures of 0.4°C (January) and 23.8°C (July) respectively and an annual precipitation of 753 mm (averages from 1971 to 2000; weather station at the village of Nohèdes).

A total of 95 plots were distributed regularly at nodes of a grid with cells 450 m on a side (not all nodes of the grid were sampled) (Fig. 1). Elevation of the plots ranged from 655 to 2252 m a.s.l. (Fig. 2). Each plot consisted of a circular area of 20 m radius in which ant nests were actively searched by experienced ant collectors. Sampling was performed between July and October 2012 and between May and August 2013. Plots were searched for a cumulative time of 40 to 180 min. Investigation time depended on habitat structure (plots with little vegetation and

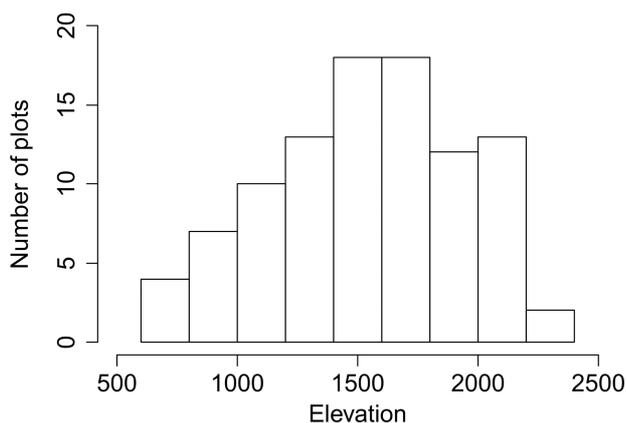


Fig. 2: Altitudinal distribution of the plots sampled on Mount Coronat.

few potential nesting sites were faster to sample) and on the diversity of ants found (sampling stopped when we noticed a strong decrease in the rate of discovery of new species). To minimize the investigator effect, sampling was performed by four collectors highly experienced in ant surveys. This procedure allows an accurate comparison of diversity indices and community composition among plots. For those species that could not be identified reliably in the field we collected a few individuals per nest for later identification under a binocular microscope (31% of the nests). Species identification followed recent taxonomic work and keys for the western Palaearctic (SEIFERT 1988, 1992, 2007, 2012, SCHLICK-STEINER & al. 2006b, SEIFERT & SCHULTZ 2009, RADCHENKO & ELMES 2010, STEINER & al. 2010, RIGATO 2011, BLATRIX & al. 2013). For the *Temnothorax* of the *luteus* species-group we followed PLATEAUX & CAGNIANT (2012) and we used the name *Myrmica scabrinodis* sensu lato, i.e., including *M. scabrinodis* NYLANDER, 1846 and *M. martini* SEIFERT, YAZDI & SCHULTZ, 2014. Pitfall trapping and nest counting are the two methods most frequently used in ant surveys. However, the data they yield are not always congruent (SCHLICK-STEINER & al. 2006a), and thus, the choice depends on the goal of the study. Pitfall trapping better reflects above-ground ecological impact because it favours epigeic species with high nest densities and long-distance foraging (SCHLICK-STEINER & al. 2006a). In contrast, nest counting better accounts for the relative abundance of the diverse life strategies, at least in temperate environments. As we focused on environmental factors as potential filters on ant communities, we preferred a more even representation of the different life-styles and chose nest counting. Nest counting was also more appropriate than pitfall trapping in our study because: (1) it allowed computation of nest abundances for each plot (all nests encountered were recorded) in contrast to pitfall traps from which species abundances do not reflect nest abundances, (2) it offered a greater efficiency in terms of species accumulation (GOTELLI & al. 2011), (3) the data it produced are less sensitive to weather fluctuations, which are strong at short time-scale under mountain climate, and (4) there is no need to visit the plots a second time (access to most plots was difficult because of steep terrain and poor track network on Mount Coronat). Ant species abundances (i.e., the number of nests per plot for each species), species rich-

ness and Simpson's reciprocal diversity index ($1/D$) were calculated for each plot.

Of the 95 plots, trees were present in 76. These 76 plots were permanent plots established for the "Protocol for dendrometric monitoring of forest reserves". This protocol is derived from that used in the European program COST action E4 "Forest Reserves Research Network" and was designed on behalf of the French ministry of ecology, sustainable development and energy by a working group of experts at the national level. For these plots, the following environmental parameters were measured in the field by R. Pimenta in the framework of the COST program: slope, exposition, basal area (total surface occupied by the cross-sections of tree trunks over 7.5 cm diameter), tree species diversity ($1/D$), and the dominant tree species (i.e., the species with the largest total basal area in the plot). A basal area of zero was assigned to the 19 plots without trees. The other parameters were not measured in these 19 plots, but slope and exposition were inferred from the digital terrain model of the French national institute of geographic and forest information (IGN).

The effects of environmental parameters on ant richness and diversity were analysed using a generalized linear model (GLM) and linear and polynomial regressions. Linear and second order polynomial models were compared with AIC. The effects of environmental parameters on ant community composition were analysed with a Redundancy Analysis (RDA). This analysis combines linear regression and principal component analysis and allows displaying plots, species and environmental parameters in the same factorial space. Species recorded only once or twice were removed to prevent analyses from being unduly influenced by rare species. Exclusion of rare species is the standard procedure for running a RDA (BORCARD & al. 2011). Hellinger transformation was applied to the species abundance matrix before analysis. Diversity (GLM) and community-composition (RDA) analyses were performed twice: once with all 95 plots (four environmental parameters: slope, exposition, elevation and basal area) and once with the 76 plots with trees (six environmental parameters: slope, exposition, elevation, basal area, tree species diversity and the dominant tree species).

A hierarchical classification of the plots based on the composition of their ant communities (rare species removed) gave additional information on the relationships between ant communities and environmental parameters. A dendrogram of the plots was obtained from the Hellinger distance matrix, using the Ward method. The Hellinger distance is the most appropriate for species abundance data (BORCARD & al. 2011).

Data analyses and figures were performed using R 3.1.0 (R CORE TEAM 2014) and the R package vegan (OKSANEN & al. 2013).

Results

A total of 1900 ant nests belonging to 74 species were recorded in the 95 plots (species are listed in Appendix S1, as digital supplementary material to this article, at the journal's web pages). Species in *Tetramorium* group *caespitum-impurum* are distinguished from each other by male genitalia (SCHLICK-STEINER & al. 2006b). Males were present in 41% of the nests and were closest to those of *Tetramorium alpestre* STEINER, SCHLICK-STEINER & SEIFERT,

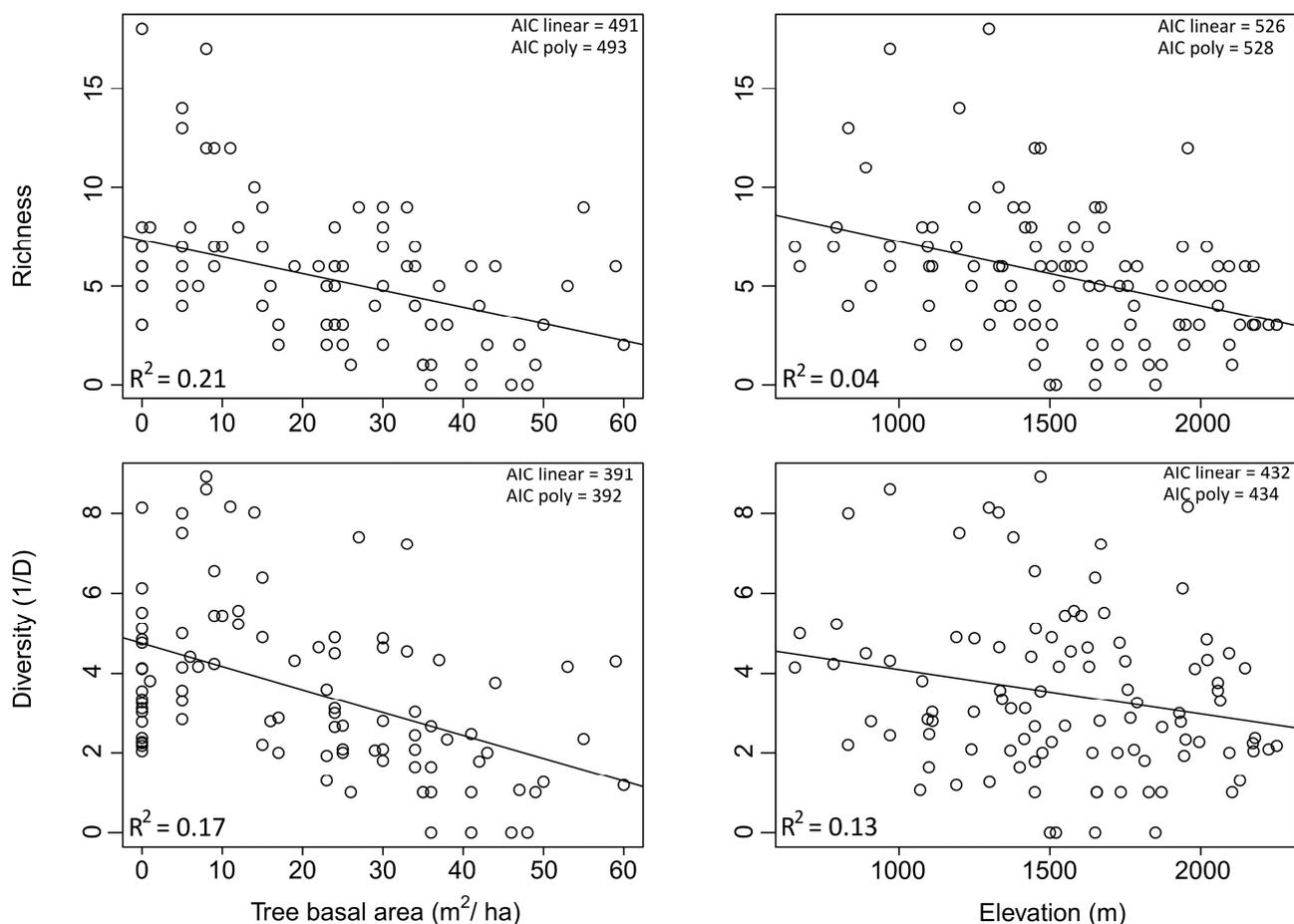


Fig. 3: Linear regression of ant species richness and diversity on tree basal area and elevation for 95 plots. AIC values are given for linear ("AIC linear") and second order polynomial ("AIC poly") models.

Tab. 1: Effects of environmental parameters on ant species richness and diversity tested with a GLM on all 95 plots (four parameters) and a GLM on the 76 plots containing trees (six parameters). Values given for each parameter are those of the F statistic. *: $P < 0.05$, ***: $P < 0.001$.

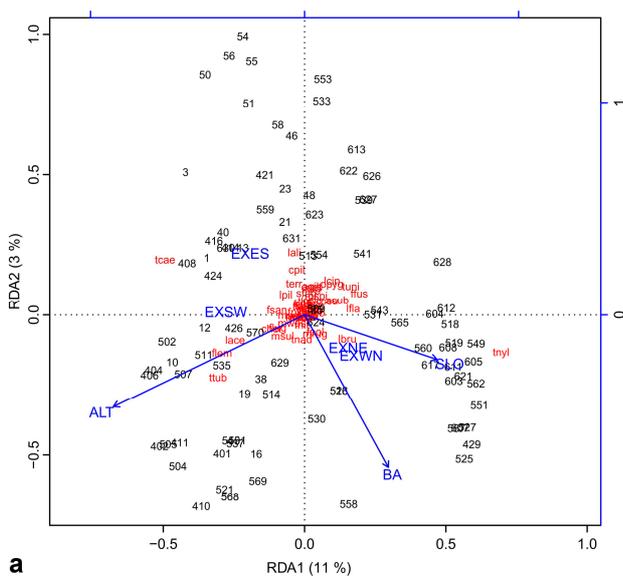
| | | Slope | Exposition | Elevation | Basal area | Dominant tree species | Tree diversity |
|----------|-----------|-------|------------|-----------|------------|-----------------------|----------------|
| 95 plots | Richness | 0.2 | 0.5 | 14.9*** | 22.7*** | | |
| | Diversity | 1.5 | 0.1 | 4.7* | 27.0*** | | |
| 76 plots | Richness | 0.1 | 0.1 | 24.3*** | 28.8*** | 2.0 | 0.2 |
| | Diversity | 1.8 | 0.3 | 14.9*** | 47.2*** | 2.1 | 1.4 |

2010, a recently described species of the *caespitum-impurum* group (STEINER & al. 2010). As the other nest samples could not be identified precisely, for analyses we considered all records of the *caespitum-impurum* group (including those with males) as one species.

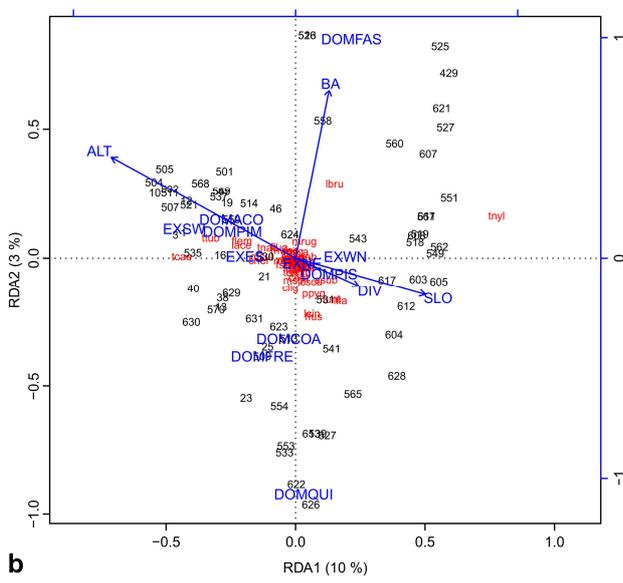
Both the GLM run on all 95 plots with four environmental parameters and the GLM run on the 76 tree-covered plots with six environmental parameters indicated that only basal area and elevation had significant effects on ant species richness and diversity (Tab. 1). Values of the F statistic indicated that basal area had the stronger effect, especially on diversity. AIC values were lower for linear than for second order polynomial models (Fig. 3). Linear regression showed that both ant species richness and diversity decreased when elevation and basal area increased

(Fig. 3). However, elevation and basal area were not significantly correlated ($R = 0.00087$, $P = 0.99$).

Fifty species were used in the RDA after removal of rare species. Analyses run on all plots and on tree-covered plots (four and six environmental parameters, and 91 and 72 plots respectively, because in four plots no nests were detected) showed a relatively weak fit to the model ($R^2_{\text{adjusted}} = 0.17$ and 0.23 respectively), but the global test was significant (10000 permutations, $P < 0.0001$). R^2_{adjusted} values of RDA are usually quite low compared with the case for other ordination methods. With six environmental parameters, there was not only a better overall fit to the model ($R^2_{\text{adjusted}} = 0.23$) than when only four environmental parameters were included ($R^2_{\text{adjusted}} = 0.17$), but also the number of significant axes of the RDA was higher (five signi-



a



b

Fig. 4: Correlation plots of the first two axes of redundancy analyses based on (a) 91 plots and four environmental parameters and (b) 72 plots and six environmental parameters. Numbers refer to plots, lower case text to ant species (for meanings of abbreviations, see Appendix S1) and upper case text to environmental parameters (ALT: elevation, BA: tree basal area, SLO: slope, DIV: tree species diversity, EX: four categories of exposition in grades (NE: 0 - 99, SE: 100 - 199, SW: 200 - 299, NW: 300 - 399), DOM: dominant tree species (QUI: *Quercus ilex*, ACO: *Acer opalus*, FRE: *Fraxinus excelsior*, FAS: *Fagus sylvatica*, COA: *Corylus avellana*, PIM: *Pinus mugo* ssp. *uncinata*, PIS: *Pinus sylvestris*). Percentages of explained variance are indicated in brackets after axes names. These percentages are adjusted values, i.e., explained variance multiplied by R^2_{adjusted} (BORCARD & al. 2011).

ficant axes, compared with three when four environmental parameters were included). In both analyses, elevation, basal area and slope explained most of the dispersion of the plots on the first two axes (Fig. 4). However, slope was negatively correlated with elevation ($R = -0.43$, $P <$

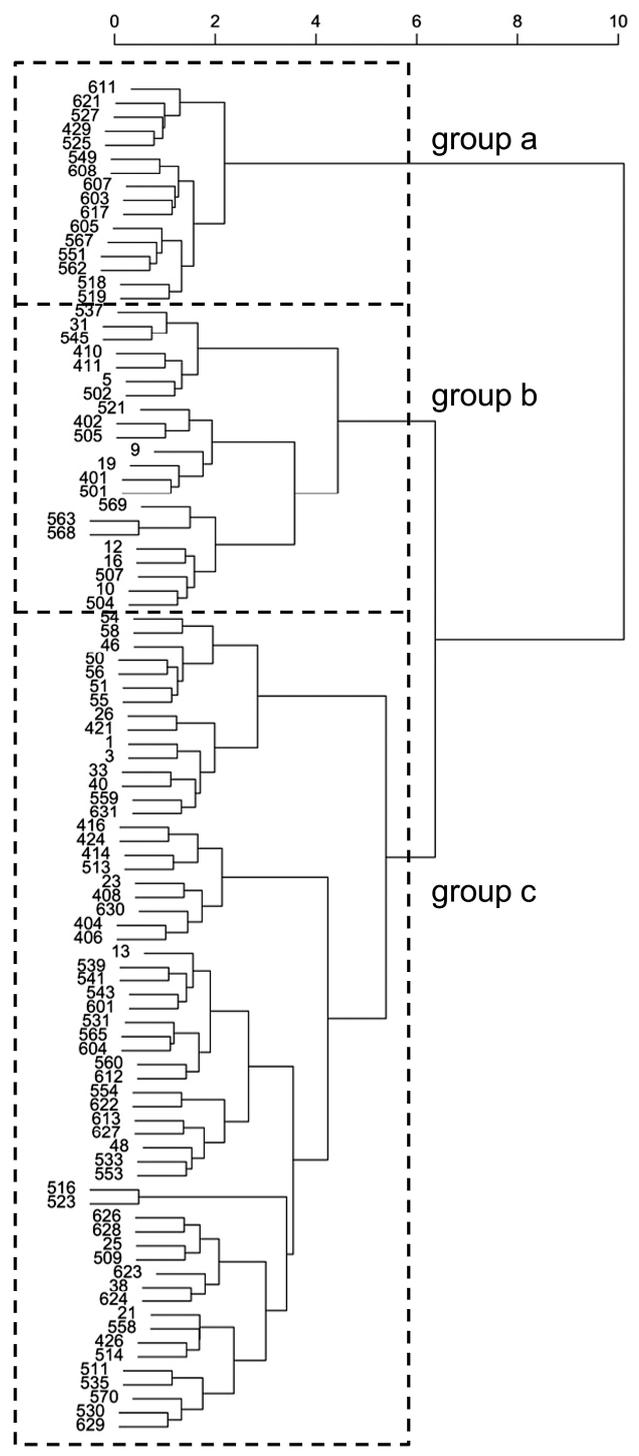


Fig. 5: Dendrogram resulting from hierarchical classification of plots based on ant species abundances (Hellinger distance, Ward's method).

0.001) in our study site. In the analysis on tree-covered plots the dominant tree species characterises axis 2, with an opposition between *Quercus ilex* LOUR. and *Fagus sylvatica* L. (Fig. 4b). However, interpretation should be cautious because there were very few plots dominated by these species (two and four respectively) and, although tree basal area was not significantly different among dominant tree species globally (Kruskal-Wallis test, $\text{Chi}^2 = 3.4$, $P = 0.19$), plots dominated by *Quercus ilex* and *Fagus sylvatica* had

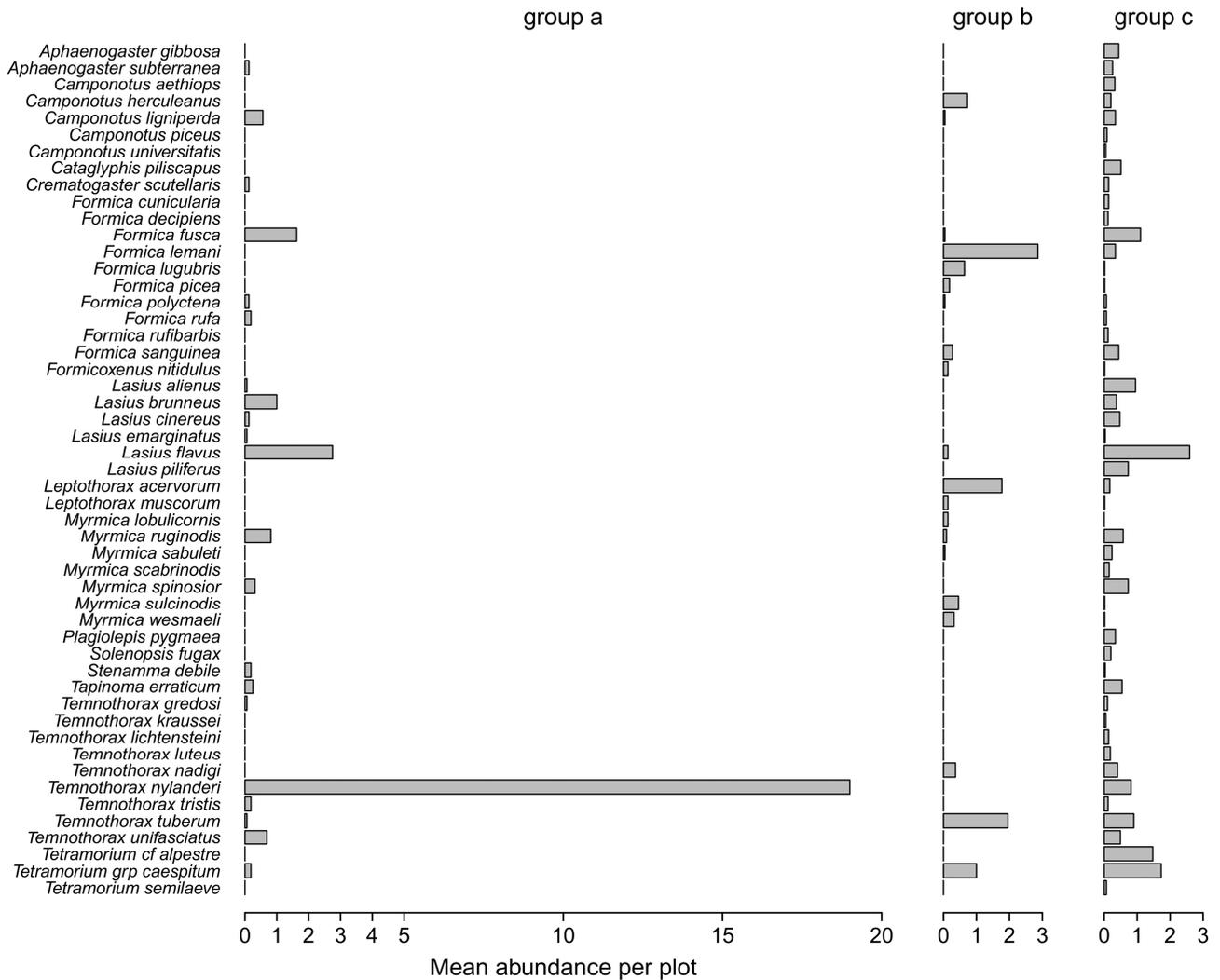


Fig. 6: Mean ant species abundances for each of the three groups of plots defined with hierarchical classification based on ant community composition.

respectively the lowest and the highest values of basal area. *Lasius cinereus* SEIFERT, 1992 and *Formica fusca* LINNAEUS, 1758 were associated with plots dominated by *Quercus ilex* and *Lasius brunneus* (LATREILLE, 1798) with plots dominated by *Fagus sylvatica*. *Temnothorax nylanderi* (FOERSTER, 1850), and to a lesser extent *Lasius brunneus*, were associated with high basal area and steep slope. In contrast, *Lasius alienus* (FOERSTER, 1850), *Cataglyphis piliscapa* (FOREL, 1901), and *Tetramorium* group *caespitum-impurum* showed the opposite trend. Three species, *Temnothorax tuberculatum* (FABRICIUS, 1775), *Formica lemani* BONDROIT, 1917, and *Leptothorax acervorum* (FABRICIUS, 1793), were very characteristic of high-elevation plots. *Camponotus herculeanus* (LINNAEUS, 1758), *Formica lugubris* ZETTERSTEDT, 1838, and *Myrmica sulcinodis* NYLANDER, 1846 showed a similar but weaker trend. In contrast, *Formica fusca*, *Temnothorax unifasciatus* (LATREILLE, 1798), *Plagiolepis pygmaea* (LATREILLE, 1798), *Lasius cinereus*, *Lasius flavus* (FABRICIUS, 1781), and *Aphaenogaster subterranea* (LATREILLE, 1798) were characteristic for low-elevation plots. All other species were very close to the centre of the plot, and thus showed no preferences or had average preferences.

The dendrogram obtained by the hierarchical classification of the plots based on the composition of their ant communities did not show straightforward discontinuity in the branching pattern (Fig. 5). We chose to recognize three groups of plots, subsequently named *a*, *b* and *c*, because the three groups thus defined reflected ecological differences; increasing the number of groups recognized made ecological interpretation difficult. Each of the three groups of plots had distinct, characteristic ant communities (Fig. 6). For describing ant communities in each group of plots we distinguished samples of *Tetramorium* group *caespitum-impurum* that could have been identified as *Tetramorium alpestre* from those that remained unidentified (i.e., samples without males), because data on the ecology of *T. alpestre* indicates it is a mountain species (STEINER & al. 2010) and this information could help interpreting the ecological characteristics of the ant community of each group of plots. Plot group *a* was remarkably well separated from the other groups in the dendrogram (Fig. 5). These plots had low ant species diversity (Fig. 7) and were dominated by *Temnothorax nylanderi* (Fig. 6). *Lasius brunneus* was mostly restricted to these plots. Group *a* plots were situated at relatively low elevations and showed a very high

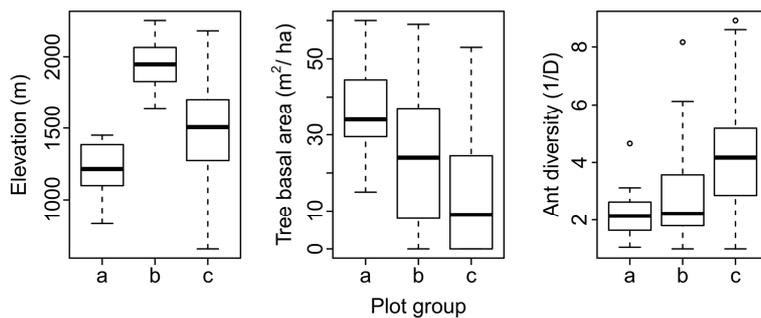


Fig. 7: Distribution of elevation, tree basal area and ant diversity for each of the three groups of plots defined with hierarchical classification based on ant community composition. Horizontal line, boxes and whiskers represent respectively median, 1st and 3rd quartiles, and lowest and highest data still within 1.5 interquartile range of the lower and upper quartiles. Outliers are plotted as individual points.

tree basal area (Fig. 7). Plots in group *b* were dominated by cold-tolerant, especially boreo-alpine, species such as *Camponotus herculeanus*, *Formica lemni*, *Formica lugubris*, *Leptothorax acervorum*, *Myrmica sulcinodis*, and *Temnothorax tuberum* (Fig. 6). These plots were located at the highest elevations and had low ant diversity (Fig. 7). Group *c* was composed of all the other plots, corresponding to a mix for which interpretation is much less clear.

Discussion

Among the six environmental parameters considered in this study (slope, exposition, elevation, tree basal area, tree species diversity and the dominant tree species), tree basal area and elevation had the strongest influence on ant species richness, diversity and community composition. Slope and the dominant tree species appeared to have effects on ant community composition but these are most likely confounding effects of elevation and of tree basal area, respectively. Indeed, in our study site, slope and elevation are negatively correlated, because the lower part is mostly composed of mountain sides and the higher part of summit plateaus. In addition, the apparent effect of dominant tree species was due to the fact that a very small number of plots were dominated by *Quercus ilex* or by *Fagus sylvatica*, stands of which have respectively the lowest and the highest basal area of the species present in our sites.

Studies on ant responses to elevation gradients are scarce in the Western Palearctic (HAGVAR 2005, GLASER 2006, HERRAIZ 2010, BERNADOU & al. 2013, 2015), despite the fact that this region has the oldest tradition of myrmecology. The relationship that we observed between elevation and ant diversity showed a linear decrease. However, the linear model did not fit as well. A possible explanation is that our plots did not follow a linear transect but were scattered over the mountain, increasing the potential influence of parameters other than elevation. In addition, the apparent effect of elevation on ant diversity results from the combination of abiotic factors that are themselves influenced by elevation. A strong correlation between elevation and ant diversity is thus not expected. For instance, BERNADOU & al. (2015) described a decrease of ant diversity with increasing elevation in two sites in the Pyrenees mountain, but the correlation was not significant. In addition, our altitudinal gradient started at 600 m. Investigation at lower elevations might thus change the shape of the curve. Some studies have documented a mid-elevation peak in species richness of various taxa (MCCAIN & GRYTNES 2010), including ants (SAMSON & al. 1997, SANDERS 2002). Mid-elevation peaks in diversity have been explained by the fact that a high proportion of lowland habitats have been disturbed by human activities or by a mid-domain effect (i.e., the mid-elevation domain combines diversity

from both low- and high-elevation domains) (MCCAIN & GRYTNES 2010). Nevertheless, in contrast to what is commonly observed in the tropics, we did not detect a dramatic drop of diversity toward the highest elevations, although our gradient reached 2400 m and covered a wide range of elevation.

In our study, the most important determinant of ant species diversity was tree basal area. Tree basal area also significantly affected ant community composition. The dendrogram obtained from the hierarchical classification of plots revealed one group (group *a*) that was particularly well differentiated from the others based on ant community composition. Plots from this group had the lowest ant diversity and were characterized by the highest basal areas, but not by the highest elevations. This indicates that basal area, or some vegetation trait correlated with it, imposes a strong constraint on both ant community composition and diversity. In our study area, which is characterized by a Mediterranean climatic influence, it appears that basal area is even more constraining than elevation. Tree basal area, a parameter that is quickly and easily measured, is a good proxy for tree cover, and therefore for the amount of sunlight that directly hits the ground or low vegetation, the two substrates where the vast majority of temperate ants forage. In similar environments not far from our study site, low basal area was shown to favour the abundance of a dominant ant species, which in turn, diluted the positive effect of habitat openness on ant diversity (ARNAN & al. 2009, BERNADOU & al. 2015). Previous studies have already highlighted the positive effect of habitat openness on ant diversity (RETANA & CERDÁ 2000, ARNAN & al. 2009, DEL TORO 2013, DEL TORO & al. 2013, BERNADOU & al. 2013, 2015). Here we propose that the limitation of radiant heat by tree cover explains this effect on ant diversity. GOTELLI & ELLISON (2002) found higher ant diversity with increasing light availability in a forested temperate environment, but lower diversity in bogs (open) than in forests. We believe this last pattern may be due to particularly high moisture at ground level in bogs, which may be detrimental to ant activity because it dissipates radiant heat at ground level. In extreme environments however, specific abiotic factors may impose stronger constraints than radiant heat. This is the case of arid environments where water availability strongly filters ant communities. As a result, ant diversity was shown to increase with elevation (SANDERS & al. 2003), a very unusual pattern.

The radiant-energy hypothesis, i.e., the hypothesis that radiant energy that heats the foraging substrate is among the factors most constraining ant diversity and community composition, provides a good explanation for local and global patterns of ant diversity. However, variation in sub-

strate use should be considered when interpreting data in the light of the radiant-energy hypothesis. Tree cover is particularly detrimental to ant diversity in temperate ecosystems (RETANA & CERDÁ 2000, ARNAN & al. 2009, DEL TORO 2013, DEL TORO & al. 2013, BERNADOU & al. 2015) because most ants forage on the ground and low vegetation.

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