



## Original article

# Monopolization of resources by ground-nesting ants foraging on trees in Mediterranean forests



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## ABSTRACT

Ant communities are generally structured by territoriality, dominance and resource monopolization, but in Mediterranean hot grassland thermal tolerance plays a more important role. The main purposes of the present research were to investigate the hypothesis that in cooler Mediterranean forests resource monopolization structures the generalist ground-nesting ant community while foraging on trees, and to learn if tree heterogeneity plays any role in this structure. In Mediterranean forests in Israel, I visually recorded and trapped ants on the forest floor and those climbing on trees of five species. Ants of 27 species were detected, while the Chao2 index indicated an asymptotic richness estimation of  $31 \pm 8.1$  species (mean  $\pm$  S.D.). The numerically dominant species were *Crematogaster lorteti* and *Tapinoma simrothi* followed by *Tapinoma israele* and *Crematogaster scutellaris*. In more than 80% of the cases, specimens of only one ant species climbed at the same time on any individual tree, and no tree was occupied by more than three species. The C-score of climbing ants was statistically higher than simulated indexes when resources were individual trees, indicating that the ants strongly monopolized each tree. No difference was detected between observed and simulated C-scores when resources were tree species. The observed index of Pianka's niche overlap indicated no species specific interaction between trees and ants. In conclusion, this study confirms that ant mosaic structure may be formed by ground-nesting ants while foraging on trees. Tree species heterogeneity did not have a selective impact on the ants nor a central role in the ant community structure.

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## 1. Introduction

Schoener (1974) argued that the habitat characteristics are one of the main segregating dimensions that structure the community. According to Shmida and Wilson (1985), habitat diversity is one of the categories of biological mechanisms which maintain species diversity. Classical niche theory predicts that heterogeneity of the environment should promote biological diversity (Davies et al., 2009; MacArthur, 1972; Oliver et al., 2010), particularly by providing various resources, and therefore it is expected to produce niche differentiations (Armbrecht et al., 2004; Levin, 1992; Santos et al., 2014). Especially plant diversity is supposed to drive

species variety of herbivorous insects (Borer et al., 2012; Castagneyrol and Jactel, 2012; Haddad et al., 2001; Novotny et al., 2006; Santos et al., 2014; Siemann et al., 1998). This trend seems to exist in temperate forests contrary to tropical forests rich in tree species where herbivory and host specificity of arboreal and free-living insects seems to be reduced (Basset, 1992; Jactel and Brockerhoff, 2007; Novotny et al., 2002). Trees do not only provide resources to herbivorous insects that directly feed on them, but they also feed insects, like ants, by the way of sap feeding insect producing honeydew (Blüthgen et al., 2000). It was shown that tree heterogeneity increased the tri-trophic trophobioses networks of plant-Hemiptera-ants (Staab et al., 2014). Given that honeydew composition varies according to both the homopteran species and their host plants (Hendrix et al., 1992; Völkl et al., 1999; Fischer and Shingleton, 2001), we can hypothesize that different species of insects may use trees from different species parasitized by homopterans, although it was demonstrated in Spain that generalist ants may exploit the honeydew from different aphid species (Alsina et al., 1988; Retana et al., 1987).

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Ants are typically territorial (Andersen, 1992; Hölldobler and Wilson, 1974), and their community is structured by ecological dominance, which is a combination between behavioural aggressiveness and numerical dominance (Cerdà et al., 2013). For example, in the tropics, the canopy of each individual tree may be occupied by a single ecologically dominant arboreal species and some tolerated subordinate ones, forming an “ant mosaic” (Majer, 1976; Majer et al., 1994; Room, 1971; Sanders et al., 2007). To date, such ant mosaics have been described in non-tropical regions only by Markó et al. (2004). This structure of arboreal ant community may be explained by competition for highly predictable resources within a given time and space, such as carbohydrates secreted by extra floral nectaries (EFNs) or honeydew producers (Blüthgen and Stork, 2007; Ribas and Schoederer, 2002).

In hot open habitats in the Mediterranean region, dominance and resource monopolization are secondary to thermal tolerance in structuring the community (Cerdà et al., 1997), while shade-tolerant species are found more common near trees (Reyes-López et al., 2003). In the cooler Mediterranean forests generalist ground-nesting ants often climb on plants to exploit temporal resources. It is unknown if they monopolize the resources in their territory, creating a possible temporary ant mosaic, when utilizing trees. Furthermore, we do not know if there is a specific species association between trees and ants or if the distribution of the ants among tree species is driven only by the occurrence of the trees in their territory.

In the present research I sought to answer the questions: Do generalist ground-nesting ants monopolize trees when foraging on them? Which species are quantitatively dominant while climbing on trees? Do the ant species niches overlap for resources? Is there a species specific association between trees and ants?

## 2. Methods

### 2.1. Research region and sites

I studied ant assemblages in six sites located in the upper central region of the Galilee Hills in northern Israel (mean annual rainfall: 600–900 mm; ca. 400–800 m above sea level), with all at the same latitude in order to minimize the effect of this geographic variable on the results (Gotelli and Ellison, 2002). The community is part of the Mediterranean biome, which is one of the most threatened in the world (Underwood et al. 2009). The sites were, from west to east: Park Goren (33°03' N., 35°13' E.), Biranit (33°03' N., 35°20' E.), Sassa (33°01' N., 35°23' E.), Tsivon (33°01' N., 35°24' E.), Dovev (33°03' N., 35°24' E.), and Baram (33°03' N., 35°26' E.). The natural vegetation of the Upper Galilee highlands is a mosaic of dense woody thicket (Mediterranean maquis) based on evergreen Palestine oak (*Quercus calliprinos* Webb) – terebinth (*Pistacia palaestina* Boiss.) community; and Mediterranean shrub steppe (bata), dominated by *Sarcopoterium spinosum* (L.). The maquis supports other tree species, which essentially follow the bedrock, soil characteristics and climatic factors (Rabinovitch-Vin, 1986), resulting in a high level of tree richness on small surfaces. In Israel, ants are represented by at least 241 species and sub-species (Vonshak and Ionescu-Hirsch, 2009).

### 2.2. Sampling methods

I actively monitored ants on forest floor and on trees. I employed two methods to monitor the ant species that climb on trees – trapping and direct observations. I used pitfall traps consisting of 50-ml test tubes filled halfway with a 50% ethylene glycol mix. At each site I attached them to the main trunk of randomly chosen trees at chest height. I placed a single trap on five individual trees of

each of the following five species: Palestine oak, terebinth, medicinal snowbell – *Styrax officinalis* L., spiny hawthorn – *Crataegus aronia* [L.] Bosc. Ex. DC, and the olive tree – *Olea europea*. The 150 traps were active for 15 days and nights in April, when ant activity is most pronounced in this region (personal observation); therefore the sampling consisted of a total of 2250 trapping days.

Ant mosaic of true arboreal ants is generally detected by canopy fogging (Blüthgen and Stork, 2007). This method was not suitable for our purpose, which was to monitor only the ground-nesting ants that were temporarily climbing on trees and not the true arboreal ants nesting in trees. Instead, I adopted Majer's (1976) method of direct observation of 400 randomly selected trees belonging to the same five tree species at the same sites in the spring (April–May). The observations were made from 7:00 AM to 11:00 AM, when the mild temperatures allowed maximal ant activity. On each tree, the same observer always counted the number of ants observed climbing from the ground onto the trunks during 2 min. Similarly, I counted the number of ants on the surface of the soil at least 2 m from each monitored tree during 2 min, to allow comparison between arboreal and ground ant activity at the same time. During the direct observations on soil and trees, I collected all the ants that I found, and preserved them in 70% isopropyl alcohol. Ant species were identified following Kugler (1984), updated to recent nomenclature (Agosti and Johnson, 2005).

### 2.3. Data analysis

#### 2.3.1. Ant species richness

To estimate asymptotic species richness I used the Chao2 index (Chao, 1984). The Chao2 is a non-parametric method preferred for colonial insects like ants to estimate species richness (Longino, 2000), based on the presence-absence record of species in each transect obtained from each method. Chao2 was calculated for the total regional species richness of the ants on floor and climbing on trees, and also separately for the total arboreal ants – in traps and during visual surveys, using EstimateS version 9 (Colwell, 2013).

To test for site differences in ant species richness, I used Statistix (2008) software to perform two single-factor ANOVAs (one for each sampling method) on the square root number of ant species (Zar, 2010), without distinguishing the tree species.

#### 2.3.2. Monopolization of trees

To confirm the monopolization of trees by ant belonging to few species, I sought a distribution pattern in which each individual tree was occupied by a dominant ant species, alone or together with one or very few subordinates. Following Gotelli (2000) and Blüthgen and Stork (2007), I employed null model analysis to confirm the co-occurrence patterns of species that had been detected by direct monitoring. I built a presence/absence (1/0) matrix with the data from the direct observations, where the rows represented ant species and each column represented an individual tree. I analysed the null species associations with null models, using the EcoSim program, Version 7.0 (Gotelli and Entsminger, 2010). The default co-occurrence index was Stone and Robert's (1990) C-score, which measures the average number of “checkerboard units” (CU) between all possible pairs of species. The number of CUs is defined as the number of species pairs in the matrix that never co-occur. The C-score is calculated as:

$$CU = (r_i - S)(r_j - S),$$

where S is the number of shared sites (here, the number of individual trees in which both members of a species pair are present), and  $r_i$  and  $r_j$  are the row totals for ant species i and j, respectively. I compared the observed C-score to the average C-score generated

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