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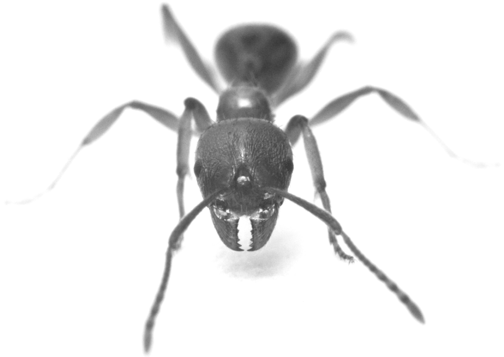
Spatio-temporal organization of sub-Mediterranean woodland ant communities (Hymenoptera: Formicidae)

Summary of the PhD thesis



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1. Introduction

Competition is traditionally considered to be one of the most important mechanisms affecting community organization in ants. Evidence for competition is provided by a number of findings, including interference behaviours between foraging workers and colonies, and the spatial and/or temporal patterns of species distributions. Emphasis is on dominance hierarchies, territoriality and its various expressions (e.g., "ant mosaics"), dominance-diversity relationships, and the impact of invasive species on native ant communities.

The stable coexistence of competing species, and thus the maintenance of local diversity, however, can be promoted by many compensatory mechanisms. Among these, the role of various dominance-related trade-offs together with spatial and/or temporal resource partitioning seems to be the most relevant, but factors that influence the outcomes of competitive interactions (e.g., the presence of parasitoids, habitat complexity, type of food source, etc.) can also be important.

Nevertheless, besides the various forms of agonistic behaviour, other behavioural mechanisms relevant to competition should also be mentioned. Tool use, for instance, may increase the ability of tool-using species to compete more successfully with other ant species. Similarly, trophobiotic relationships between ants and various hemipterans (e.g., aphids, coccids, hoppers, etc.) may not only induce behavioural changes in the ant host, but also indirectly affect the organization of the community by enhancing the success of ecologically dominant ant species.

2. Aims

The main objective of the research presented in the thesis was to explore the composition and spatio-temporal organization of two sub-Mediterranean woodland ant communities. According to my overall hypothesis, competition for different resources (nesting sites and/or food) plays an important role in the organization of the communities examined, resulting in, inter alia, (1) the regular spatial distribution of ant nests and the increase of regularity in their spacing in time, (2) the density-dependence of nest spacing patterns, (3) the significance of trade-offs in resource use and thermal tolerance, (4) the spatial and/or temporal (daily and/or seasonal) segregation of foraging workers of different species, and (5) the occurrence of linear (transitive) dominance hierarchies.

Besides the above-mentioned major studies on community organization, some minor studies were focused on *Prenolepis nitens* and *Aphaenogaster subterranea*, the dominant species of the ant communities examined. In these studies, I investigated the winter activity of *P. nitens*, and the tool-using behaviour of *A. subterranea* in retrieving food and its association with the cixiid planthopper, *Reptalus panzeri*.

3. Materials and methods

3.1. Study sites

Studies were carried out in two woodland habitats of the Balaton Uplands in the Transdanubian Mountains in mid-western Hungary. The first study site, Péter Hill is situated in the middle of the Balaton Uplands, extending 2 km southwest from the village of Csopak to Balatonfüred-Arács. The second study site, Mogyorós Hill is located ca. 17 km north-east from Péter Hill between the villages of Litér and Királyszentistván. In both sites, field work was conducted on the south-facing hill slopes.

The vegetation on the south-facing slope of Péter Hill is composed of a mosaic of karst shrub (*Cotino-Quercetum pubescentis*) and downy oak forest (*Vicio sparsiflorae-Quercetum pubescentis*) with downy oak (*Quercus pubescens*) and manna ash (*Fraxinus ornus*) as dominant tree species. The south-facing slope of Mogyorós Hill is dominated by planted black pine (*Pinus nigra*) stands mixed with young deciduous trees, mostly manna ash.

3.2. Sampling methods

In both sites, ant nests were mapped in three randomly placed plots of 7 m × 7 m in four time periods from spring to autumn 2010. Within each plot, the soil surface, leaf-litter, fallen, rotten branches and twigs, fruits (e.g., acorns), galls and empty snail shells were thoroughly searched to locate ant nests. The coordinates of ant nests were measured to the nearest centimeter, and the type of nesting sites (i.e., under stone, in the soil, leaf-litter, etc.) was recorded.

Similarly to nest mapping, bait experiments were conducted in both sites in four time periods from spring to autumn 2011. For baiting, honey and tuna fish were used as bait substances to give choice between carbohydrate and protein food. During the experiments, three sets of baits, separated by ca. 15 m were randomly located. Each set consisted of five baits placed on the ground along a line transect at 3-m intervals, and five on tree trunks at breast height. Ants were surveyed every hour for 12 consecutive hours (7 am-7 pm) in spring and summer, and every hour for 10 consecutive hours (8 am-6 pm) in autumn, ca. 45 minutes after the placement of baits. During each ca. 1-minute observation period, species identity, number and localization of visiting workers at baits were recorded, and the following behaviour patterns were distinguished: (1) feeding on bait substances ("feeding"); (2) being present at baits without any significant activity ("present"); (3) initiating an attack against an individual of another species/colony ("attacking"); (4) escaping from the bait caused by the presence or attack of an individual of another species/colony ("escaping"). Together with the hourly measurement of ant activity, surface air temperature and ground temperature at 15 cm depth were measured with a digital thermometer.

The winter activity of *P. nitens* was assessed in the oak forest using baiting and quadrat sampling on seven days between December 2012 and March 2013. The method of baiting, the number and placement of baits, etc. were the same as discussed in the former section, however, with shorter surveys, i.e., every hour for five consecutive hours from 10 am to 3 pm. The activity of foraging workers was estimated also by using three randomly placed observation plots of 50 cm × 50 cm in size, separated by ca. 15 m. The number of workers seen inside or entering the quadrats and the type of prey carried over a 3-minute period were recorded every hour for five consecutive hours (10 am-3 pm). Together with the hourly measurement of foraging activity, surface air temperature and ground temperature were measured as mentioned above.

The tool-using behaviour of *A. subterranea* in retrieving food was assessed in the pine forest using bait experiments on four days in August 2013. For baiting, honey and petroleum jelly were used as bait substances. Petroleum jelly was used to test the hypothesis whether a non-food viscous liquid presenting a potential hazard of drowning or becoming entangled elicits the same response and behaviour from foraging workers as in the case of liquid food. During the experiments, four sets of baits, separated by ca. 15 m were randomly located. Each set consisted of five baits placed on the ground along a line transect at 3-m intervals. On each day, ants were surveyed every 20 minutes for four consecutive hours from 6:20 am to 10:20 am, ca. 45 minutes after the placement of baits. During each ca. 1-minute observation period, the number and localization of visiting workers at baits were recorded, and the following behaviour patterns were distinguished: (1) feeding on bait substances ("feeding"); (2) being present at baits without any significant activity ("present"); (3) dropping tools into bait substances ("dropping"); (4) adjusting the position of tools ("adjusting"); (5) transporting food-soaked tools from the bait back to the colony ("transporting").

The association of *R. panzeri* with ants was investigated in the oak forest using five randomly placed plots of 3 m × 3 m on five occasions from spring to autumn 2011. Within each sampling plot, the soil surface, leaf-litter, fallen, rotten branches and roots of trees and shrubs were thoroughly searched to locate ant nests and planthopper nymphs located outside nests. Every time an ant nest was found the following parameters were recorded: (1) the type of nesting site (i.e., under stone, in the soil, leaf-litter, in fallen branches, etc.); (2) the estimated size of the colony (small, medium, large) on the basis of the number of workers/brood and the extent of the nest; (3) the presence, number, estimated size (small, medium, large) and exact location of individual planthopper nymphs inside the nest; (4) all the species of shrubs and trees close to the nest the roots of which could be present in the nests. On three occasions after field studies, fragments of colonies of *A. subterranea* and planthopper nymphs from nests were separately collected and transferred to the laboratory. Within a few hours of collecting in the field, nymphs were placed in Petri dishes with rootlets and nest material, and then workers of *A. subterranea* were added and the reactions of both species to one another were recorded.

3.3. Data analysis

The spatial pattern of ant nests was analyzed using the Clark and Evans' nearest neighbour method. This analysis was carried out both for the nests of the most abundant species (≥9 nests per plot) and for all nests found in the sampling plots. In the former case, the nearest neighbour index (*R*) was measured intraspecifically, on the basis of the nearest conspecific neighbour distances, and also on the basis of the nearest neighbour distances, i.e., when the species identity of the nearest neighbour was not considered during the analysis. Differences between the nearest conspecific and heterospecific neighbour distances in each time period, and differences in the nearest conspecific and heterospecific neighbour distances among time periods were analyzed to determine whether colonies preferred the vicinity of conspecific or heterospecific neighbours, and whether this preference varied seasonally. These comparisons were also carried out both for the nests of the most abundant species and for all nests found in the sampling plots.

Null-model analyses were used to determine whether the measure of spatial and temporal overlap observed between the most abundant and frequent species pairs visiting baits differed significantly from chance expectation. To quantify patterns of temporal (diurnal and annual) and spatial overlap (i.e., the measure of co-occurrence at baits), I calculated the Renkonen similarity index and the C-score index. To compare the discovery ability of the most common species, I calculated the following measures: (1) percentage of visited baits where the given species was the first to arrive; (2) percentage of only those baits permanently occupied by a given species where it was the first to arrive; (3) time until a bait was discovered by a given species, whether it was first to arrive or not. Feeding efficiency was calculated as the ratio of the number of feeding individuals to the number of all individuals present at the bait, and it was compared separately by food type between the most common species pairs. To compare the interspecific interactions of species that were more frequently found to be co-occurring and interacting with other species (participating in ≥10 interactions resulting in expulsion from baits), the following behavioural categories were considered: (1) coexistence without confrontation with individuals of another species/colony ("coexistence"); (2) agonistic response (e.g., biting, chemical secretions, etc.) with mutual (e.g., fighting) or non-mutual aggression not leading to expulsion from baits ("aggression"); (3) passive or aggressive expulsion of individuals of another species/colony from baits ("expulsion"); (4) escape from baits elicited by the presence or aggression of individuals of another species/colony ("escape"). To determine the relative dominance of a given species, I calculated a dominance index for each species that were participating in ≥10 interactions resulting in expulsion from baits. The linearity of dominance hierarchies was quantified using the Landau index. To assess the significance of linearity in dominance relationships, I used a randomization test developed by de Vries.

4. Main results

4.1. Spatio-temporal patterns of nest density and dispersion

During the surveys, a total of 427 nests of 9 ant species were recorded in the oak forest, and 351 nests of 15 species in the pine forest. The most abundant and frequent species were *P. nitens* and *A. subterranea* in the oak forest, and *A. subterranea*, *Lasius emarginatus* and *Formica fusca* in the pine forest.

Contrary to my hypotheses, (1) the nests of the most abundant species were mostly randomly distributed intraspecifically, and all nests mapped inside each plot also showed a random spatial distribution in most cases; (2) except for a single case, no significant positive correlation was found between nest density and the degree of spatial regularity; (3) the spatial regularity of nests did not increase during the season, in fact, the distribution pattern of nests did not change significantly (pine forest), or changed from regular to random (oak forest). Overall, the nests were mostly strongly aggregated interspecifically, and the nearest heterospecific neighbour distances proved to be significantly shorter in most cases than the nearest conspecific neighbour distances.

Generally, the nearest inter-nest distances showed significant variations during the season in both habitats. Although this variation was revealed in a relatively varying manner and measure in the case of individual species, it was usually expressed as the increase of nearest inter-nest distances, in close connection with the decreasing of nest density from spring to autumn. In the case of two species, *P. nitens* and *L. emarginatus,* however, a completely different trend was observed. In the case of the former species, nest density was highest in spring and in late summer and autumn, while in the case of the latter, nest density reached its maximum in early summer. Considering that the foraging activity of both species was the highest in the same periods as well, the most likely reason for the seasonal expansion may be that the colonies of these species split into several subunits occupying separate nests in certain periods of the year, or workers open up more nest entrances in these periods. These may contribute to the extension of the foraging area of colonies, and to the decrease of search time and distances traveled by foraging workers between the food source and the nest.

The mostly random spatial distribution of nests, and the lack of density-dependent spacing can be explained by the following considerations: (1) suitable nesting sites may not be a limiting factor in these habitats, so the abundance and dispersion of these determine the distribution pattern of nests; (2) the mortality of colonies may not be density-dependent but spatially random, resulting in random patterns of spatial distribution whether the original pattern was aggregated, random or regular; (3) various environmental factors may influence the distribution pattern of nests either directly or indirectly through density-dependent processes; (4) the seasonal relocation of colonies together with seasonal polydomy may give instability to nest spacing patterns, whose relatively rapid change prevent the formation of strong interactions between neighbouring colonies.

4.2. Spatio-temporal patterns of foraging activity

During baiting trials in the oak forest, more than 100,000 individuals of 12 ant species were recorded. The most abundant (with highest number of individuals recorded) and frequent (occupying most of the baits) species was *P. nitens*. In the pine forest, nearly 20,000 individuals of 13 ant species were recorded at baits. The most abundant species was *A. subterranea,* and the most frequent species was *F. fusca*.

Contrary to the proposed hypotheses, (1) no evidence was found for either the dominance-discovery trade-off or the dominance-thermal tolerance trade-off during baiting trials, and (2) there was no significant segregation in diurnal activity patterns of species that commonly visited the baits.

Seasonal segregation seemed to be important in the oak forest, where the seasonal overlap between the two locally ecologically dominant species, *A. subterranea* and *P. nitens*, was significantly less than expected by chance. While the former species reached its seasonal activity peak in early summer, the latter proved to be most active in the cooler periods of the year, in spring and autumn.

Spatial segregation seemed to be supported in both habitats by the following observations: (1) species recorded at baits differed significantly on whether they visited baits placed on the ground or on tree trunks more frequently; (2) in the case of a number of species pairs, co-occurrence at baits was significantly less frequent than expected by chance for those periods when both members of these pairs showed relatively higher seasonal activity.

Contrary to the fact that dominant and subordinate species could be well differentiated from each other in both habitats based on dominance rank orders, the linearity of dominance hierarchies did not represent a significant departure from chance. This is probably due to the high number of unknown dominance relationships, given that members of some species pairs, owing to their strong spatial segregation and/or less frequent occurrence, never confronted each other at baits.

The most aggressive reactions and exclusions from baits were clearly demonstrated by *A. subterranea* in both habitats. The high behavioural dominance of this species in these habitats can be explained by (1) its high local abundance and frequent occurrence (i.e., high numerical dominance), (2) its spatial and/or temporal (seasonal) segregation from other species with a similar degree of behavioural dominance (e.g., *P. nitens*, *L. emarginatus*), and (3) the slight presence and/or impact of aggressive, territorial species (oak forest: *Liometopum microcephalum*, *Crematogaster schmidti*; pine forest: *Formica pratensis*). The overall success of *A. subterranea* may also be further augmented by its unique tool-using behaviour and by its close association with the cixiid planthopper *R. panzeri*, as discussed below.

4.3. Winter activity of *Prenolepis nitens*

Based on my study it seems that similarly to *Prenolepis imparis* but unlike any other syntopic ant species, *P. nitens* does not maintain a strict hibernation, and remains active above-ground all winter. The lowest surface air and ground temperatures at which workers were active were only 1.3 °C and 2.5 °C, respectively, at baits, and 0.9 °C and 2.5 °C in quadrats. During the winter period, ground temperature seems to be the critical factor regulating activity for this species.

Stress tolerance in these cryophilic species may serve not only to reduce encounters with potential competitors, but also to provide additional resources in the form of cold stressed prey.

4.4. Tool use of *Aphaenogaster subterranea*

The tool-using behaviour of the foraging workers of *A. subterranea* visiting honey baits consisted of three distinct components that were usually performed by different individuals: (1) selecting, picking up, carrying and dropping tools into the liquid food until its surface was entirely covered; (2) adjusting the position of tools brought by other workers in order to be soaked fully with food; (3) removing and transporting food-soaked tools from the bait back to the colony.

Although the number of workers manipulating tool items was significantly lower than the number of workers performing other activities, there was a positive correlation between them, i.e., the more workers visited the baits, the more exhibited some form of tool-using behaviour.

Materials most commonly used as tools were particles of soil and easily moveable, broken fragments of plant materials (e.g., bits of pine needle, cone and bark), which were collected directly from the side of the baits.

Tool-using workers also dropped some debris into petroleum jelly at 60% of the baits, however, at a much lower intensity and quantity than in the case of honey.

The main adaptive advantages of this tool-using behaviour may be (1) the more effective protection of the food source, (2) the more efficient transport of liquid food, and (3) a better chance of avoiding interference with other ant species.

4.5. Association of *Aphaenogaster subterranea* with cixiid planthoppers

Overall, a total of 110 planthopper nymphs were located in ant nests, 96% of which occurred in the nests of *A. subterranea*. The mean number of nymphs in the nests of *A. subterranea* was 3.42 (± 2.84 SD), the largest group consisted of 12 individuals. The number of planthopper nymphs found in the nests of *A. subterranea* colonies of different sizes did not differ significantly.

It is suggested that the association is facultative for *A. subterranea* as more nests were recorded without than with planthopper nymphs or traces of nymphs. On the other hand, the association of *R. panzeri* with its ant partner appears to be obligatory as most of the nymphs were found inside ant nests, and those nymphs found outside nests were almost in all cases accompanied by workers of *A. subterranea*.

Although no collecting of honeydew or direct physical contacts between the workers of *A. subterranea* and the nymphs of *R. panzeri* were observed in the study, it is likely that there is some kind of mutualistic relationship between them, as (1) ant workers did not show predatory or agonistic behaviour towards planthopper nymphs; (2) nymphs, even though saltatory, did not attempt to escape from ants; (3) nymphs located outside of ant nests were generally visited by the foraging workers of *A. subterranea*, even when they were in the nests of other ant species.

Therefore, although only supported by circumstantial evidences, the close association of *A. subterranea* and *R. panzeri* may represent a true mutualistic relationship between the two species beyond simple cohabitation, thereby providing a constant source of honeydew and benefits going along with it for colonies of *A. subterranea* in these habitats.

5. Publications related to the topic of the thesis

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6. Publications not directly related to the thesis

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