

Differential impact of two dominant *Formica* ant species (Hymenoptera, Formicidae) on subordinates in temperate Europe

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Academic editor: Jack Neff | Received 29 February 2016 | Accepted 17 April 2016 | Published 27 June 2016

<http://zoobank.org/F8E45D32-7A35-40C9-A10A-07FBD7A0B871>

Citation: Trigos Peral G, Markó B, Babik H, Tăușan I, Maák I, Pálfi Z, Ślipiński P, Czekes Z, Czechowski W (2016) Differential impact of two dominant *Formica* ant species (Hymenoptera, Formicidae) on subordinates in temperate Europe. Journal of Hymenoptera Research 50: 97–116. doi: 10.3897/JHR.50.8301

Abstract

Competition is one of the basic mechanisms shaping ant assemblages. Dominant territorial species are known to restrictively influence the traits of subordinates in various ways. However, there could be differences in the effects of dominants due to differences in their colony structure, lifestyle and also behaviour. We tested this hypothesis in natural circumstances in an area where a *Formica exsecta* Nyl. supercolony neighbours a strong population of the European slave-maker *F. sanguinea* Latr. For the purpose of our study three different sites were selected: one dominated by *F. exsecta*, a neighbouring site dominated by *F. sanguinea*, and a third site where both species co-occurred. We analyzed the structure of subordinate ant communities based on nest counts, and by recording the activity of ants at baits. Based on our findings the structure of ant communities differed significantly among the three sites. The *F. exsecta* site was characterized by the lowest nest density of subordinates, especially in the case of aggressive species as *Lasius platythorax* Seifert. At baits even the simple presence of the dominant limited the abundance and occurrence of subordinates. In contrast, no such negative effect could be revealed at the *F. sanguinea* site. The community of the mixed site showed intermediate features in many respects. Generally, the supercolonial

F. exsecta had a bigger influence on the ant community than the slave-making *F. sanguinea*. On the other hand, our findings revealed a slight protective role of the territorial *F. exsecta* for potential slave species to *F. sanguinea*. The current study underlines the importance of differences between dominant ant species in shaping differentially ant communities even within the same restricted area.

Keywords

Formica exsecta, *Formica sanguinea*, baits, community structure, competition, interspecific hierarchy, nest density, slavery, territoriality

Introduction

Most of the concepts regarding the assembly rules of animal communities point to competition as a crucial factor in shaping their composition and structure (MacArthur 1972, Wiens 1983, Farris et al. 2015, McFarlane Tranquilla et al. 2015, Sunarto et al. 2015). This is supported for ants as well by several case studies (e.g. Savolainen and Vepsäläinen 1988, Pisarski and Vepsäläinen 1989, Cerdá et al. 1998, Parr and Gibb 2010, Czechowski et al. 2013, Maák et al. 2014, Ślipiński et al. 2014, Dejean et al. 2015, Spotti et al. 2015) and the work reviewed quite recently by Cerdá et al. (2013). Specifically, ant communities in temperate zones are organized hierarchically and a crucial role in shaping them can be attributed to ecologically and behaviourally dominant species. Dominant species can restrictively structure local communities in various ways, from interference and exploitative competition to direct predation on lower-ranked species, both quantitatively (decreasing nest densities and colony sizes of subordinates) and qualitatively (reducing species richness by competitive exclusion and altering the dominance structure), but also with regards to the spatial patterns of the nests (e.g. by forced resource partitioning, nest moving, etc.) (Higashi and Yamauchi 1979, Cherix and Bourne 1980, Pisarski 1982, Pisarski and Vepsäläinen 1989, Savolainen and Vepsäläinen 1988, 1989, Savolainen et al. 1989, Savolainen 1990, 1991, Vepsäläinen and Savolainen 1990, Hölldobler and Wilson 1990, Punttila et al. 1991, 1996, Sanders and Gordon 2003, Czechowski and Markó 2005, Adler et al. 2007, Czechowski et al. 2013, Markó et al. 2013, Rzeszowski et al. 2013, Ślipiński et al. 2014).

Typically, at least in Euro-Asian boreal and temperate zones, the top dominants of ant communities are territorial species (sensu Pisarski 1982), i.e. those which actively protect the boundaries of their whole foraging areas against other territorials (Pisarski 1980, Vepsäläinen and Pisarski 1982, Pisarski and Vepsäläinen 1989). In temperate Europe, such territorial dominants, already well-known for their competitive impact on subordinate ants, are the wood ant species of the *Formica rufa* group (subgenus *Formica* s. str. L.) (Savolainen and Vepsäläinen 1988, 1989, Savolainen et al. 1989, Savolainen 1990, 1991, Punttila et al. 1991, 1996, Czechowski and Markó 2005), species of the subgenus *Coptoformica* Müll. (genus *Formica* L.) (Czechowski 1975, Pisarski 1982, Pisarski and Vepsäläinen 1989), the dendrophilic *Lasius* (*Dendrolasius*) *fuliginosus* (Latr.) (Czechowski et al. 2013, Markó et al. 2013, Ślipiński et al. 2014),

and *Liometopum microcephalum* (Panzer) (Petráková and Schlagamerský 2011). Colonies of territorial species (either allo- or conspecific) do not share the same territory, but non-territorial species can nest and forage within the dominant's territory, however with diverse limitations. Their colonies are the centres of the spatial organization in ant communities through their differential effects on subordinate species, which are 'allowed' only to nest at certain distances from the nest of the territorial species – the farther away are the nests of the subordinates, the stronger could be the competition between the two species (Savolainen and Vepsäläinen 1988, Pisarski and Vepsäläinen 1989). The impact of territorials on subordinates may further be enhanced by specific social strategies, such as the formation of new colonies through budding, which leads to the development of a network of related nests over a larger area (so-called supercolonies – see e.g. Helanterä et al. 2009, Robinson 2014 for reviews), a well-known strategy in many territorial wood ants (Higashi and Yamauchi 1979, Cherix and Bourne 1980, Rosengren et al. 1985), but also in members of the subgenus *Coptoformica* (Pisarski 1982, Czechowski 1975, 1977, Markó et al. 2012).

Within subordinates, two competition levels are distinguished: (a) encounter species, which are fairly aggressive and usually manage to monopolize (defend) single food sources, and (b) submissive species, which defend only their nests (Vepsäläinen and Pisarski 1982). Although they can manage to survive in the territory of dominants, subordinates are restrictively affected by territorials, and, in general, they fare better outside than within territories of dominant species (Savolainen 1990, 1991). On the other hand, in certain situations, nesting inside a dominant territory can even be good for certain species. Members of the subgenus *Serviformica* For. (genus *Formica*) are slave species for the facultative slave-maker *Formica* (*Raptiformica*) *sanguinea* Latr. Potential slave colonies may profit from the proximity of strong dominants since these can stop the raiding columns of *F. sanguinea* or force them to change their route when protecting their own territory. Such a positive effect of territorials has been reported for several species of wood ants of the *F. rufa* group (*F. rufa* L., *F. polyctena* Först., *F. aquilonia* Yarr., *F. lugubris* Zett.) for *F. fusca* L. and *F. lemani* Bondr., and known slave species *F. sanguinea* (Punttila et al. 1996, Czechowski 1999, 2000, Czechowski and Vepsäläinen 2001, Czechowski and Markó 2006, Väänänen et al. 2010). A similar mechanism may also work, at least to some extent, in the case of *Serviformica* species enslaved by the obligate slave-maker *Polyergus rufescens* (Latr.) (Czechowski 2006).

The differences among dominant species regarding their effect on subordinates may vary depending on their lifestyle (slave-maker vs non-slave-maker), colony structure (mono- vs polydomous), and on their foraging strategies (narrow vs wide food spectrum). The differential effect of dominants on subordinates are best revealed when dominant species occur syntopically (in the same habitat), consequently, the basic species pool that could make up the ant community is the same. Therefore, if the differences between the dominants are negligible, the differences between the ant communities occurring in their territories/areas should also be minor. In order to test this hypothesis, an appropriate natural set-up is needed, with the long-term co-occurrence of territorial allospecific neighbours (see e.g. Czechowski et al. 2013). Recent field

studies performed on the largest European polydomous system of the territorial *Formica exsecta* (Markó et al. 2012) yielded the discovery of a large population of the slave-maker *F. sanguinea*, also a dominant species, neighbouring the above-mentioned supercolony. This unique natural set-up of two dominant neighbours from the same genus, yet with a different colony structure (supercoloniality vs mono- or oligodomy) and lifestyle (non slave-maker vs slave-maker) offered the chance to perform a comparative study. In the framework of the current study, we proposed an analysis of the structure of ant communities in the area of these two dominants, and formulated the following questions: (1) are there any differences between the structure of ant communities of the two neighbouring dominant *Formica* species' territory/area, (2) are there any differential effects of these two dominants on the foraging strategies of subordinate species, (3) do the abundance and foraging strategy of members of the subgenus *Serviformica*, known as a slave species of *F. sanguinea*, differ within and outside the *F. sanguinea* area?

Materials and methods

Study species and sites

The main subjects of the study are two dominant ant species: *Formica* (*Coptoformica*) *exsecta* and *Formica* (*Raptiformica*) *sanguinea*.

Formica exsecta is a fairly common North-Palaeartic mound-building territorial species, a typical forest-ecotone polytope dwelling in forest margins and clearings, thinned young growth, overgrowing meadows and glades, etc. Its colonies number several thousand to tens of thousands of workers and occur in two, mono- and polygynous social forms. Polygynous colonies may grow through nest splitting into polydomous systems, often with more than 100 nests (so-called supercolonies). Additionally, colonies may be established through the temporary social parasitism of members of the subgenus *Serviformica*. The optimal home range of foraging workers from a single nest does not exceed a few meters. They are aggressive and predacious ants, which also feed on honeydew (Pisarski 1982, Seifert 2000, Hughes 2006, Erős et al. 2009, Csata et al. 2012).

Formica sanguinea is a common South-Palaeartic species, a polytope of warm and dry habitats, both forested and open areas; generally its ecological preferences widely overlap with those of the former species. It nests in decaying tree stumps, partly covered with dry plant material and also in the ground, often under stones. In general, colonies, usually functionally monogynous, number up to several tens of thousands of workers. It is a facultative socially parasitic species which enslaves workers of the subgenus *Serviformica*; the range of its slave raids may reach 100 m (usually < 50 m). They are very aggressive and predatory ants; during their raiding period they do not respect the boundaries of other species' territories (Czechowski 2000, Hughes 2006). The territoriality of *F. sanguinea* is a moot point (see the Discussion).

As habitat niches of *Formica exsecta* and *F. sanguinea* overlap each other to a considerable degree, colonies of these two species often co-occur.

Our study area was a vast semi-moist meadow of the *Molinia caeruleae* W. Koch alliance [with, among others, *Molinia caerulea* (L.) Moench, *Deschampsia caespitosa* (L.) P. B., *Festuca pratensis* Huds., *Nardus stricta* L. and *Juncus* sp.], densely overgrown with small birch saplings, located in the southern part of the Giurgeului depression (46°36'N; 25°36'E; 780 m a.s.l.) in the eastern Carpathians, Transylvania, Romania. The meadow is fairly intensely grazed by cows for most of the year. This is the location of the largest known European polydomous system of *Formica exsecta*. The supercolony contains 3,347 permanent nests over an area of nearly 22 ha (i.e. the nest density is ca. 153/ha) (Markó et al. 2012). A population of *F. sanguinea* was recently detected, with a small number of *F. cunicularia* Latr. and *F. rufibarbis* F. slaves, within the same habitat near the area occupied by the supercolony.

Three sites were selected within the area for the purpose of our study (Fig. 1): (1) a site clearly dominated by *Formica sanguinea* right at the border of the *F. exsecta* polydomous system (referred to as the *F. sanguinea* site; 32 *F. sanguinea* nests on ca. 3210 m² with 0.01 nests/m², and four *F. exsecta* nests with 0.001 nests/m²), (2) a neighbouring patch within the *F. exsecta* territory with a single *F. sanguinea* nests (referred to as the *F. exsecta* site; 68 nests on ca. 5780 m² with 0.012 *F. exsecta* nests/m², and one *F. sanguinea* nest with 0.0002 nest/m²) and (3) a site with interspersed nests of both *F. sanguinea* and *F. exsecta* (referred to as the mixed site; eight *F. sanguinea* on ca. 2685 m² with and 0.003 nests/m², and 80 *F. exsecta* nests with 0.03 nests/m²). Within the whole study area, the meadow was homogeneous in respect of the vegetation, surface configuration and sun exposure.

The study area was not part of any nature protection area and no specific permits were required to carry out the field studies.

Sampling methods

Nest densities of different subordinate ant species were obtained using the biocoenometric method, by carefully investigating 15 quadrats of 9 m² at each of the three study sites. The quadrats were randomly selected by a blindfolded person in the field, they did not border each other, and they were at least 2 m from any *Formica exsecta* nest (Fig. 1). A sample of workers was collected for precise identification from each nest found. Identification of ant species was carried out with the key of Czechowski et al. (2012). Field work was carried out between 17 and 21 June 2010.

Baiting is commonly used to study the foraging pattern of ants around their nests and species' foraging strategies. It is also an appropriate method for determining the hierarchical positions of particular species within an assemblage (e.g. Czechowski 1979, 1985, Czechowski and Pisarski 1988, Parr and Gibb 2010, Petráková and Schlaghamerský 2011, Markó and Czechowski 2012). As the food preferences of ants may change seasonally, we provided a mixture of two different kinds of bait:

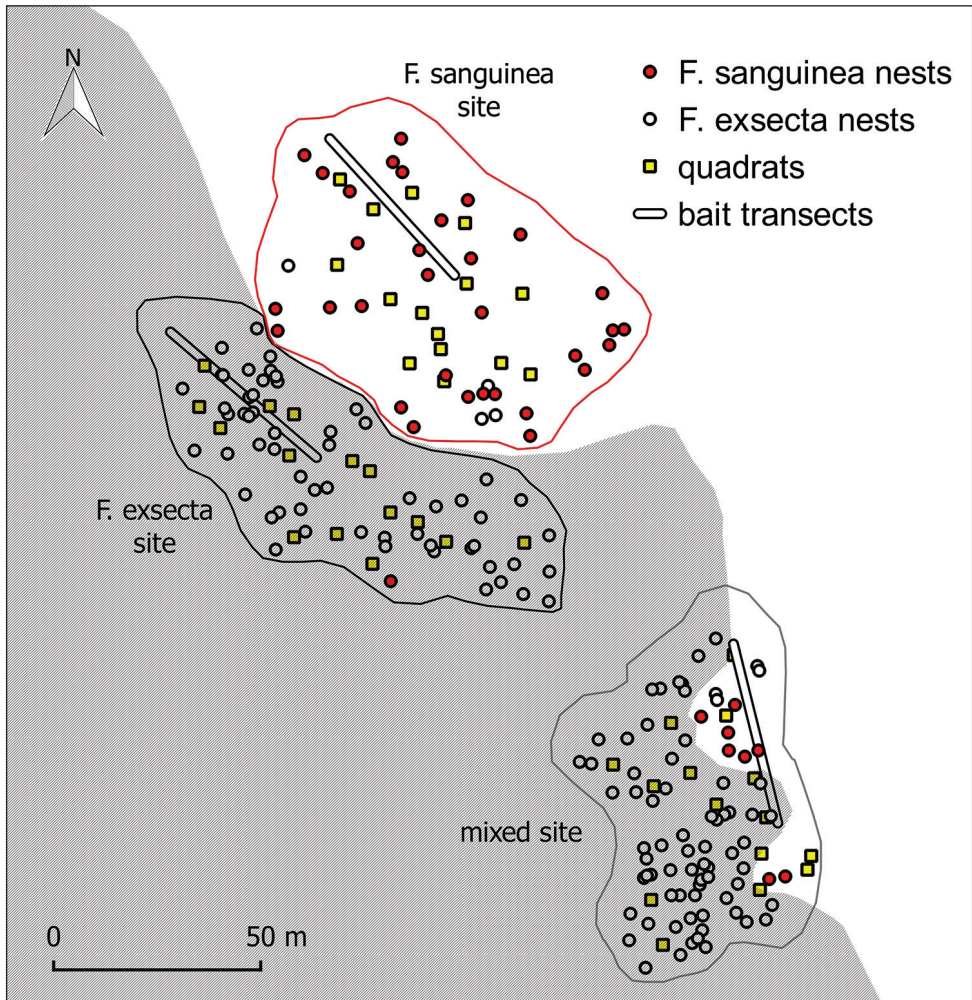


Figure 1. Map of the study area (*F. exsecta* nests outside the delineated sites are not marked out; grey area – compact area of the *F. exsecta* supercolony).

tuna fish flakes as a source of animal protein food and a water solution of mixed-flower honey as a source of carbohydrates. Altogether, 10 observation plots were distributed along linear transects at each of the three study sites (Fig. 1), and the baits were put out in the centre of each plot, separated from the next plot by 2 m, and placed at least 2 m from any *Formica exsecta* or *F. sanguinea* nest and any previously surveyed plot. The bait portions of ca. 3 cm diameter were placed in the centre of a round green plastic plate of 10 cm diameter. Baiting observations were carried out on 8 July 2010. Observations were carried out in two periods: between 10⁰⁰ and 12⁰⁰ AM, and between 5²⁰ and 7²⁰ PM. Each period consisted of six observations of

1 min, separated by 20 minute breaks. During each observation, the number and species of ants appearing at the baits were recorded, with the exception of *Myrmica* spp., where species level identification could not be performed under field conditions. The baits were put out 10 minutes before each period of observation (morning and afternoon) and left there until the end of the period when they were retrieved and the plates cleaned.

Data analyses

The differences in the abundance of different ant species among sites were revealed by the use of the Kruskal-Wallis test, followed by Tukey and Kramer post-hoc tests. The diversity of ant communities was calculated with the Shannon-Wiener entropy index (\log_2), using data for individual quadrats and baits respectively for nest count and bait data, while differences among sites for these parameters were revealed by using the Kruskal-Wallis test, followed by the Tukey and Kramer post-hoc tests separately for nest count and bait data. In order to determine the differences among the ant assemblages of the three sites, permutational multivariate ANOVA (perMANOVA, 10000 permutations) was applied both for nest count and bait data, while Nonmetric Multidimensional Scaling (NMDS) was used to visualize the three assemblages, both in the case of nest and bait data. The SIMPER test was performed to determine the contribution of each species to dissimilarities between ant communities.

The Generalized Linear Mixed Model approach (GLMM, binomial, maximum likelihood) was applied to analyze the effect of dominant species on the presence and absence of subordinate species at baits. The abundance of *Formica sanguinea* and *F. exsecta* workers present at baits were introduced as variables, along with their presence vs absence data as factors, next to the type of the site (*F. sanguinea*, *F. exsecta*, mixed) as a factor. The period and time of the observation as well as bait ID were introduced as nested random factors. A similar approach (GLMM, Poisson error, maximum likelihood) was applied to separately test the effect of dominants on the abundance of subordinates. The number of all subordinates was pooled together, since they showed a low abundance separately (see the Results). The same model structure was used as above.

All statistical analyses were carried out using the R 3.1.2 statistical package (R Core Team 2015). Multiple pairwise comparisons in the case of the Kruskal-Wallis tests concerning diversity indices were performed using the Tukey and Kramer post-hoc test after Nemenyi with the *PMCMR* R-package (Pohlert 2015). Permutational multivariate ANOVA, NMDS and the SIMPER test were carried out with the *vegan* R-package (Oksanen et al. 2013). GLMMs were performed using the *glmer* function in the *lme4* R-package (Bates et al. 2014). Post-hoc Tukey-tests for sequential comparison among factor levels when performing GLMM were carried out with the *glht* function in the *multcomp* R-package (Hothorn et al. 2015).

Results

Species composition and abundance

During the quadrat survey, 171 nests were found belonging to 11 subordinate ant species in addition to the two dominant species (i.e. *Formica sanguinea* and *F. exsecta*) (Table 1). Five subordinate species occurred at every site studied [*Tetramorium* cf. *caespitum* (L.), *Myrmica scabrinodis* Nyl., *M. vandeli* Bondr., *M. schencki* Viereck, and *Lasius flavus* (F.)]. Total nest density of co-occurring ant species was 1.8 times higher at the *F. sanguinea* than at the *F. exsecta* site, whereas it was intermediate at the mixed site (Table 1). The most abundant subordinate species was the subterranean *L. flavus* followed by *M. scabrinodis* on every study site (Table 1).

Only three aggressive encounter species were found: *Lasius platythorax*, *Tetramorium* cf. *caespitum* and *Formica rufibarbis*, and none of them were present in high densities at the site (territory) of *F. exsecta*. The three sites differed mainly in the nest density of two encounter species: *L. platythorax* and *T. cf. caespitum* (Table 1). Nest density of the former was relatively high at the *F. sanguinea* site, whereas the latter had a higher density at the mixed site. Nest density of all submissive species [*Myrmica* spp., *Leptothorax acervorum* (F.) and *Serviformica* spp.] taken together was the highest at the *F. sanguinea* site, owing mainly to the trends noticeable in *Myrmica* species (Table 1).

The ant community of the *Formica sanguinea* site was significantly more diverse than the *F. exsecta* site, while the mixed site had an intermediate position (Kruskal-Wallis $\chi^2 = 7.83$, $p = 0.02$; Fig. 2). The structure of the ant assemblages also differed significantly among the three studied sites (perMANOVA $F_{1,40} = 3.51$, $p = 0.006$), mostly with regards to the ant community of the *F. sanguinea* site, while seemingly the communities of the other two sites were quite similar (Fig. 3). According to the results of the SIMPER analysis, most of the dissimilarities (ca. 70%) among the three sites could be contributed mostly to three common species: *Lasius flavus*, *Myrmica scabrinodis* and *L. platythorax*, except for the *F. exsecta* vs mixed site, where *T. cf. caespitum* took the place of *L. platythorax* in this respect (Table 2).

Foraging strategies and competitive effects

Besides *Formica sanguinea* and *F. exsecta*, foragers of other species were also present at the baits (Table 3). The highest abundance of ants at baits was observed at the *F. exsecta* site, exclusively due to the efficient recruitment of *F. exsecta* workers to the food sources (Table 3). As expected, *F. sanguinea* was present at baits in its site, though in a surprisingly low number, whereas it was totally absent from the *F. exsecta* site; in turn, *F. exsecta* was absent in the *F. sanguinea* site. Both species exploited baits, though, at the mixed site (Table 3).

Different trends were detected in the abundance of two aggressive (encounter) species: *Lasius platythorax* and *Tetramorium* cf. *caespitum*. The former occurred in similar

Table 1. Nest densities (mean number per 9 m² ± SD) of subordinate ant species and their proportions (%) in the three study sites.

| Species | <i>F. sanguinea</i> site | <i>F. exsecta</i> site | Mixed site |
|--|--------------------------|------------------------|--------------------|
| | mean ± SD % | mean ± SD % | mean ± SD % |
| <i>Tetramorium</i> cf. <i>caespitum</i> (L.) | 0.33 ± 0.49 6.4 | 0.2 ± 0.56 7 | 0.67 ± 1.05 20 |
| <i>Leptothorax acervorum</i> (F.) | – | 0.07 ± 0.26 2.3 | – |
| <i>Myrmica scabrinodis</i> Nyl. | 1.13 ± 1.13 21.8 | 0.53 ± 0.92 18.6 | 0.73 ± 1.1 22 |
| <i>Myrmica vandeli</i> Bondr. | 0.47 ± 0.99 9.0 | 0.47 ± 0.74 16.3 | 0.13 ± 0.35 4.0 |
| <i>Myrmica schencki</i> Viereck | 0.27 ± 0.8 5.1 | 0.07 ± 0.26 2.3 | 0.13 ± 0.35 4 |
| <i>Myrmica lobicornis</i> Nyl. | – | 0.13 ± 0.35 4.7 | 0.07 ± 0.26 2 |
| <i>Myrmica ruginodis</i> Nyl. | 0.07 ± 0.26 1.3 | – | – |
| <i>Lasius flavus</i> (F.) | 2.00 ± 1.81 38.5 | 1.33 ± 1.54 46.5 | 1.40 ± 0.99 42 |
| <i>Lasius platythorax</i> Seifert | 0.87 ± 0.74 16.7 | 0.07 ± 0.26 2.3 | – |
| <i>Formica cunicularia</i> Latr. | 0.07 ± 0.26 1.3 | – | 0.13 ± 0.35 4 |
| <i>Formica rufibarbis</i> F. | – | – | 0.07 ± 0.26 2 |
| All subordinate species | 5.21 | 2.87 | 3.33 |
| All epigeal subordinate species | 3.21 | 1.54 | 1.93 |

Table 2. Results of the SIMPER analysis: the overall dissimilarity between study sites, the average contribution of subordinated ant species to overall dissimilarity (Dissimilarity contribution), their mean abundances in the compared sites (Mean 1 and Mean 2), and the cumulative percentages of contributions.

| Sites (dissimilarity) | Species | Dissimilarity contribution (%) | Mean 1 | Mean 2 | Cumulative contribution (%) |
|--|-------------------------|--------------------------------|--------|--------|-----------------------------|
| <i>F. sanguinea</i> vs. <i>F. exsecta</i> (70.13) | <i>L. flavus</i> | 20.95 | 2 | 1.54 | 29.88 |
| | <i>M. scabrinodis</i> | 13.49 | 1.13 | 0.62 | 49.13 |
| | <i>L. platythorax</i> | 12.27 | 0.87 | 0.08 | 66.63 |
| | <i>M. vandeli</i> | 9.44 | 0.47 | 0.54 | 80.11 |
| | <i>T. cf. caespitum</i> | 6.13 | 0.33 | 0.23 | 88.85 |
| <i>F. sanguinea</i> vs. Mixed (67.83) | <i>L. flavus</i> | 18.83 | 2 | 1.5 | 27.76 |
| | <i>M. scabrinodis</i> | 13.11 | 1.13 | 0.78 | 47.1 |
| | <i>L. platythorax</i> | 12.21 | 0.87 | 0 | 65.11 |
| | <i>T. cf. caespitum</i> | 9.33 | 0.33 | 0.71 | 78.88 |
| | <i>M. vandeli</i> | 6.18 | 0.47 | 0.14 | 88 |
| <i>F. exsecta</i> vs. Mixed (65.81) | <i>L. flavus</i> | 20.35 | 1.54 | 1.5 | 30.92 |
| | <i>M. scabrinodis</i> | 14.38 | 0.62 | 0.79 | 52.79 |
| | <i>T. cf. caespitum</i> | 11.16 | 0.23 | 0.71 | 69.75 |
| | <i>M. vandeli</i> | 8.48 | 0.54 | 0.14 | 82.64 |
| | <i>M. schencki</i> | 3.46 | 0.08 | 0.14 | 87.91 |

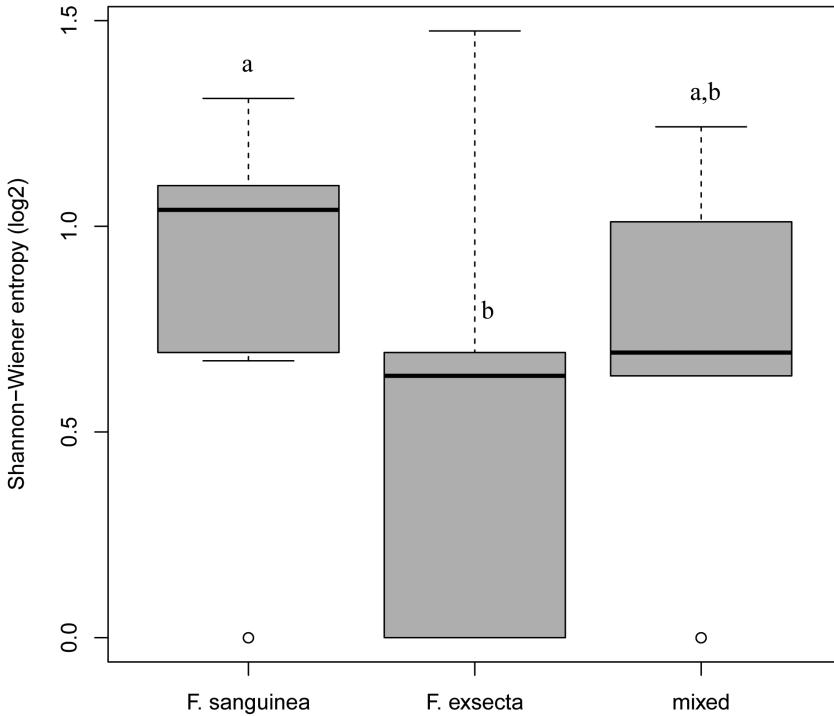


Figure 2. Diversity of the ant communities within the study sites based on nest surveys (medians, quartiles, min–max values and outliers). Survey performed on 9 m² quadrats (N = 15 in each site). Different letters indicate significant differences among groups.

Table 3. Mean number of ant individuals per baits (\pm SD) for each study site and their relative proportions (%) to other ant species at the same site.

| Species | <i>F. sanguinea</i> site | <i>F. exsecta</i> site | Mixed site |
|----------------------------------|---------------------------|----------------------------|--------------------------|
| | mean \pm SD % | mean \pm SD % | mean \pm SD % |
| <i>Tetramorium cf. caespitum</i> | 31.6 \pm 96.78 36.5 | – | 10.6 \pm 21.49 32.0 |
| <i>Myrmica</i> spp. | 2.1 \pm 3.96 2.4 | 0.2 \pm 0.42 0.1 | 4.0 \pm 3.83 12.1 |
| <i>Lasius platythorax</i> | 52.2 \pm 83.48 60.3 | 52.2 \pm 120.86 29.6 | – |
| <i>Formica cunicularia</i> | 0.6 \pm 1.9 0.7 | 3.4 \pm 4.03 1.9 | 1.8 \pm 3.16 5.4 |
| <i>Formica sanguinea</i> | 0.1 \pm 0.32 0.1 | – | 1.9 \pm 2.56 5.7 |
| <i>Formica exsecta</i> | – | 120.4 \pm 100.65 68.3 | 14.8 \pm 35.67 44.7 |
| All subordinate species | 86.5 \pm 111.43 99.9 | 55.8 \pm 121.5 31.6 | 16.5 \pm 22.75 49.7 |
| | 86.6 \pm 111.35 100 | 176.6 \pm 102.94 100 | 33.2 \pm 36.19 100 |

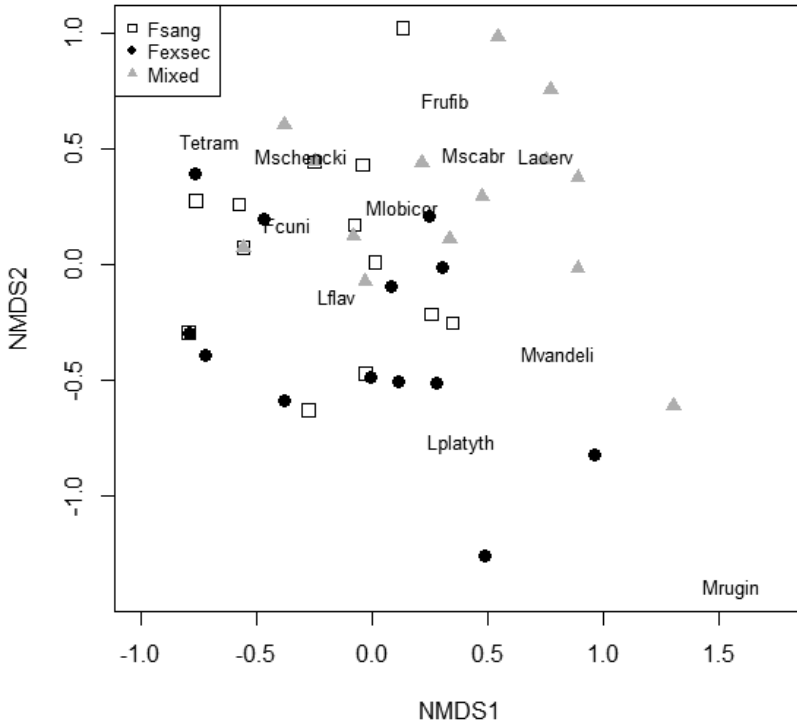


Figure 3. NMDS graph of the ant communities within the study sites based on nest survey (stress = 0.172).

numbers at baits in the *Formica exsecta* and *F. sanguinea* sites, whereas it was absent from the mixed site (Table 3). In turn, *Tetramorium* cf. *caespitum* was absent from the *F. exsecta* site, while it was the second most abundant ant in the two other sites (Table 3). The abundance of potential *F. sanguinea* slave species, such as *F. cunicularia*, gradually increased from the *F. sanguinea* site to the mixed one and then to the *F. exsecta* site (Table 3).

The highest diversity was found at baits in the mixed site (Kruskal-Wallis $\chi^2 = 9.11$, $p = 0.011$) followed by the significantly lower diversities of *Formica sanguinea* and *F. exsecta* sites, which did not differ significantly from each other based on the post-hoc test result (Fig. 4). There were no differences between the three sites in the qualitative-quantitative composition of foraging ants (perMANOVA $F_{1,29} = 1.83$, $p = 0.12$), however, baits in the *F. exsecta* territory seemed to stand apart from all other sites due to the marked presence of *F. exsecta*, while the presence of subordinate species was more characteristic for the *F. sanguinea* and the mixed sites (Fig. 5).

According to the results of the GLMM analysis, *Formica exsecta*'s abundance ($z = -3.09$, $p = 0.002$) and presence ($z = -2.32$, $p = 0.02$) had a significant negative effect on the occurrence of subordinates at baits, while the abundance of *F. sanguinea* did not play a major role ($z = -1.72$, $p = 0.08$), but its presence did have a positive influence on the occurrence of subordinates ($z = 2.13$, $p = 0.033$). There were no differences

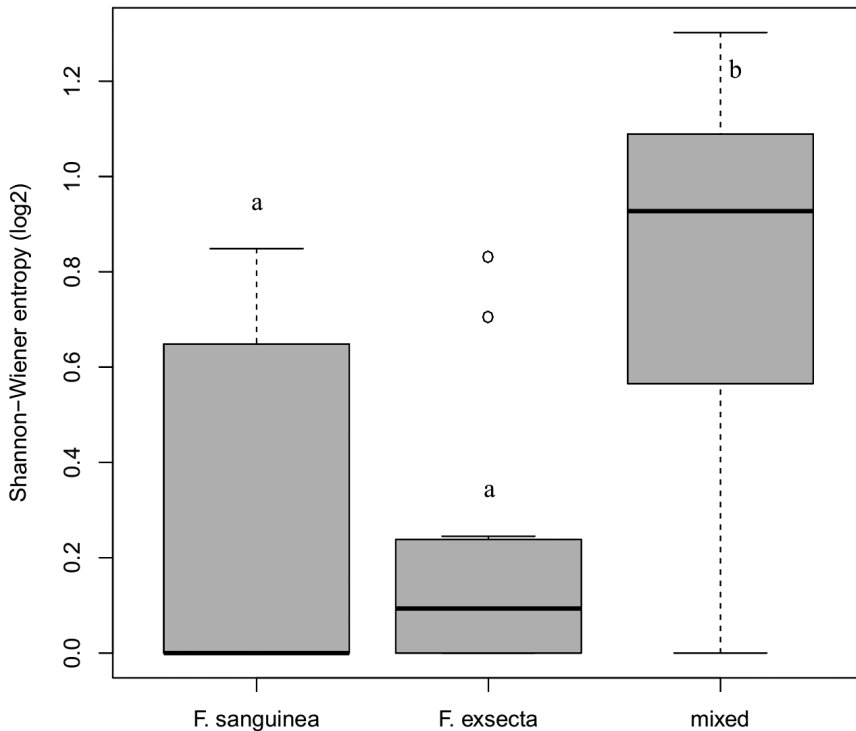


Figure 4. Diversity of the ant communities within the study sites based on bait observations (medians, quartiles, min–max values and outliers). Different letters indicate significant differences among groups.

between the *F. sanguinea* and the *F. exsecta* sites with regards to the frequency of the occurrence of subordinates ($z = 1.99, p = 0.11$). Also, no difference was found between the *F. sanguinea* and the mixed site in this respect ($z = -1.8, p = 0.16$), but subordinates were significantly less frequent at baits in the mixed site compared to the *F. exsecta* site ($z = -3.18, p = 0.004$).

Generally, a similar pattern with smaller adjustments was found when analyzing the effect of dominants on the abundance of subordinates at baits. In addition to the abundance of *Formica exsecta* ($z = -8.33, p < 0.0001$), even its simple presence ($z = -2.01, p = 0.044$) had a significant negative effect on the abundance of subordinates. On the other hand, *F. sanguinea*'s abundance ($z = 0.04, p = 0.96$) and presence ($z = 0.96, p = 0.33$) had no significant effect. The abundance of subordinates also showed significant differences among the three study sites ($z \geq 9.92, p < 0.0001$).

Discussion

The main factors which shape biodiversity and structure of animal communities are, besides habitat heterogeneity (see e.g. MacArthur and MacArthur 1961, Hölldobler

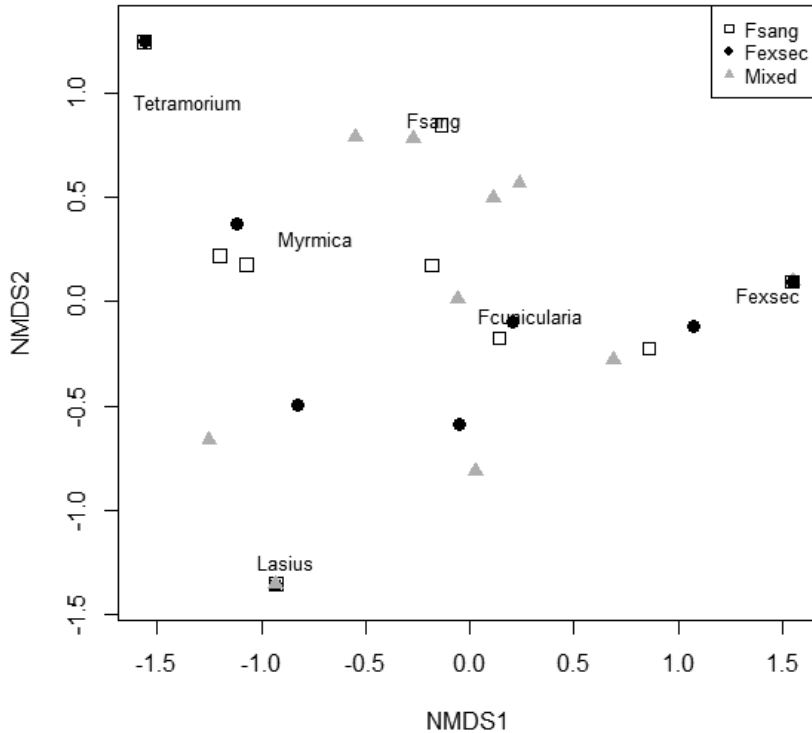


Figure 5. NMDS graph of the ant communities within the study sites based on bait observations (stress = 0.114).

and Wilson 1990, Tews et al. 2004, Ossola et al. 2015), intra- and interspecific relationships, such as competition and social parasitism. The importance of the latter is well known in ants (Savolainen and Vepsäläinen 1988, Hölldobler and Wilson 1990, Andersen 1992, Ryti and Case 1992, Cerdá et al. 1997, Czechowski and Markó 2006, Scharf et al. 2011, Ślipiński et al. 2011, 2014). Colonies of dominant species, especially territorial ones, play a crucial role, as organizing centres of the ant community, by limiting the establishment of colonies of subordinate species within dominant territories or by managing their accessibility to various resources (Savolainen and Vepsäläinen 1988, Pisarski and Vepsäläinen 1989, Andersen 1992, Bestelmeyer 2000, Lester et al. 2010, Cerdá et al. 2012, 2013, Czechowski et al. 2013). In our study, we revealed considerable differences among ant communities living in areas within the same habitat, but dominated by two dominant species with clearly different features.

The species composition of the studied ant communities was quite similar among all three sites, but differences were found in the abundance of different ant species, and also in the diversity of ant communities. In almost all respects the *Formica sanguinea* site was superior housing the most diverse ant community. Thus, despite the low chance of interaction with *Lasius flavus* due to its subterranean lifestyle, the lowest density of *L. flavus* nests was recorded in the *Formica exsecta* territory, which could be

the result of the establishment of *F. exsecta* colonies on the top of their soil mounds, with the gradual extermination of *L. flavus* colonies (Pisarski 1982). This species was followed by *Myrmica* spp. with a low level of aggression compared to *L. platythorax* and *Tetramorium* cf. *caespitum*, while the lowest abundance was recorded for members of the subgenus *Serviformica*, being both a slave species to *F. sanguinea* and the host of temporary social parasitism caused by *F. exsecta* fundatrices (Czechowski et al. 2012). Generally speaking, there was an increase in the abundance of aggressive and submissive species in the mixed territory where *F. exsecta* and the slave maker species showed lower abundance or were absent.

Usually, the exploitation patterns of food resources at the *Formica exsecta* site was in agreement with the general rules concerning hierarchy patterns, where the dominant species, especially a territorial one, monopolizes the area and its resources (Savolainen and Vepsäläinen 1988, Savolainen et al. 1989). In the *F. exsecta* site the absence of *T.* cf. *caespitum* at baits, known as an aggressive species (e.g. Brian et al. 1966, 1979) with a quick reaction towards intruders (Dobrzański and Dobrzańska 1975) and with the ability to exploit habitat resources effectively (Brian et al. 1966), might have been caused by its general avoidance of the dominant species during foraging (see Cerdá et al. 2012). On the other hand, contrary to *Formica exsecta*, as other authors have already shown before (e.g. Czechowski 1999, 2000, Czechowski and Markó 2006, Ślipiński et al. 2011), *F. sanguinea* behaved as a considerably weaker competitor, exploiting the baits much less actively than e.g. *Lasius platythorax* and *Tetramorium* cf. *caespitum*, which succeeded in exploiting the baits within its area quite heavily. The strongest difference in the exploitation pattern of baits is shown by the results obtained from the mixed territory, where the presence of almost all species at baits increased, with the exception of *Formica exsecta*, which exhibited the highest frequency and abundance in its own exclusive territory.

The low number of *Formica sanguinea* foragers at baits, especially in relation to the numbers of workers of other ant species, requires additional explanations. Recent studies on the foraging strategy of *F. sanguinea* have already shown, that this species seems to be less competitive towards subordinates to the south (e.g. Romania) than in the northern parts of the species range in Europe (e.g. Finland) (P. Ślipiński et al., in prep). One of the major signs of its weaker competitiveness is its reduced presence at artificial baits, as also confirmed by our present observations. However, it is possible that at least some of the *F. cunicularia* workers present at baits were individuals enslaved by *F. sanguinea*, and these *de facto* acted as foragers of the latter. Since, generally, slaves fulfill intranest tasks in colonies (Kharkiv 1979a,b, see also Czechowski 1996), the abundance of slaves foraging at baits could anyhow be quite low.

Territorial ants can hold off raiding columns of *Formica sanguinea* to some extent, and in this way directly protect possible slave species against their enslaver. This protective effect would manifest itself when there was a significantly greater abundance of slave species within, rather than outside of wood ant territories of the *F. rufa* group (Punntila et al. 1996, Czechowski 2000, Czechowski and Vepsäläinen 2001, Czechowski and Markó 2006, Väänänen et al. 2010). However, this is not generally valid for all territorials, since, e.g., no measurable protective effect of the territorial *Lasius fuliginosus*

towards the *F. fusca* slave species was detected by Ślipiński et al (2014), despite cases of direct interference of the latter during *F. sanguinea* raids (Czechowski 1999, 2000). In our study area, two potential slave ant species (and, at the same time, potential hosts of the temporary social parasitism of *F. exsecta*) occurred, both members of the subgenus *Serviformica*: *F. cunicularia* and *F. rufibarbis*. The former is a typical submissive species, the latter is an aggressive encounter species. Due to this, the relations of each of them with both local dominant species, i.e. *F. exsecta* and *F. sanguinea*, might proceed differently. On one hand, the submissive, weakly competitive *F. cunicularia* should be less restrictively treated by the territorial *F. exsecta* than the more competitive *F. rufibarbis*. On the other hand, colonies of the aggressive *F. rufibarbis* (see Mori et al. 2001) should be much less prone to being destroyed by *F. sanguinea*, and they should also be more resistant to being taken over by young *F. exsecta* queens than colonies of the submissive *F. cunicularia*. So, one could expect that these differences in behaviour might be reflected in differences in the distribution of the two subordinate species. However, both species were very scarce in the study area. In total, only three nests of *F. cunicularia* and one nest of *F. rufibarbis* were found. At the baits, only *F. cunicularia* foragers occurred, most abundantly within the *F. exsecta* site. At the remaining sites (both with *F. sanguinea*), they were generally scarce, and what is more, at least some of them may have been *F. sanguinea* slaves. This result may suggest some type of protective effect of the territorial *F. exsecta* on this slave species against the slave-maker.

While the decisive effect of *Formica exsecta* as a typically territorial species on the structure of ant communities is quite evident, this question still remains open regarding *F. sanguinea*. In the literature, the latter is commonly handled in a similar manner as the territorial *Formica* s. str. and *Coptoformica* species (Vepsäläinen and Pisarski 1982, Savolainen et al. 1989, Punttila et al. 1996, Czechowski 2000, Czechowski and Markó 2006, Väänänen et al. 2010). However, our findings seem to contradict the similarly strong territorial (*sensu* Pisarski 1982) nature of *F. sanguinea*. The fact that some *F. sanguinea* nests can occur in the vicinity of *F. exsecta* nests (see the mixed site) also emphasizes the reduced territoriality of *F. exsecta*. Other field observations point in this direction as well. For example, in the Białowieża Forest (N-E Poland), a very strong *F. sanguinea* colony was observed to peacefully coexist with a fairly large *F. exsecta* colony over several years, nesting just ca. 3 m from an edge of the mound of the latter (W. Czechowski, unpubl.). Also, the above mentioned recent case study on the competitive strategy of *F. sanguinea* (P. Ślipiński et al., in prep.) strongly suggests the non-territoriality of this aggressive and undoubtedly influential species.

The results of this study underscore the importance of differences between dominant ant species in differentially shaping ant communities, even within the same limited area.

Acknowledgements

We are indebted for the Apáthy István Society for the housing during the field works. The study was carried out with the support of scientific cooperation between the Polish

Academy of Sciences and the Romanian Academy. This work was supported by a grant of the Romanian National Authority for Scientific Research and Innovation, CNCS – UEFISCDI, project number PN-II-RU-TE-2014-4-1930.

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