



Unexpected distribution of subordinates around nests of the wood ants

I.E. Maák^{a,d,*}, I. Sondej^b, O. Juhász^{a,c}, G. Trigos-Peral^d, A. Tenyér^a, J. Camera^e,
W. Czechowski^d

^a Department of Ecology, University of Szeged, Közép fasor 52, H-6726, Szeged, Hungary

^b Department of Natural Forests, Forest Research Institute, Park Dyrekcyjny 6, 17-230, Białowieża, Poland

^c Doctoral School in Biology, Faculty of Science and Informatics, University of Szeged, Közép fasor 52, H-6726, Szeged, Hungary

^d Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza St 64, 00-679, Warsaw, Poland

^e Department of Life Sciences and Systems Biology, University of Turin, via Accademia Albertina 13, 10023, Torino, Italy

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ABSTRACT

The hierarchical organization of multi-species ant communities can be determined by the colony size and worker density-dependent differences in behaviour, recruitment efficiency, and aggressiveness between colonies of different species. In this study, we compared the competitive effects of two territorial wood ant species, *Formica rufa* and *F. polyctena*, on the ant species subordinated to them (encounterers and submissives) that nest close-by their mounds. The nests of subordinates were mapped in 10 m² plots around the mounds of each of the two wood ant species, situated at a distance of 10, 20 and 30 m in four directions. The most abundant subordinate species were two *Myrmica* species: *M. rubra* and *M. ruginodis*. Interestingly, the nests of subordinates had an even diversity, density and distribution along with the distance from the wood ant mounds. The wood ant presence had a species-specific negative effect on some of the subordinate species, which can be in relation with the smaller mound sizes in *F. rufa* compared to *F. polyctena*. Based on our results it seems that subordinate species, due to their adaptability, might tolerate the circumstances close-by the wood ant mounds by changes in their strategies, foraging behaviour, and switching to the use of alternative food sources, like corpses of wood ants present in high abundance. Although these might not allow reaching normal colony size and reproduction, they may allow the colonies to survive while maintaining relatively large nest densities.

1. Introduction

Interspecific competition (mainly for food sources and nesting places) plays an important role in shaping ant communities in temperate regions (Reznikova, 1982; Savolainen and Vepsäläinen, 1988; Savolainen et al., 1989; Punttila et al., 1996; Braschler and Baur, 2003; Sanders and Gordon, 2003; Adler et al., 2007; Cerdá et al., 2013; Czechowski et al., 2013). Differences in behaviour, recruitment efficiency and aggressiveness that depend on colony size and worker density are reflected in a hierarchical organization of multi-species ant communities (Savolainen et al., 1989; Cerdá et al., 2013). According to the concept of K. Vepsäläinen and B. Pisarski (Vepsäläinen and Pisarski, 1982; Pisarski and Vepsäläinen, 1989), the hierarchy consists of three main competition levels. The highest level is constituted by territorial species whose colonies defend (in addition to their nests) their entire foraging areas against foreign conspecific colonies and colonies of other territorial species. The two lower levels are created by species subordinate to

territorials: intermediate level by encounter species, which defend against competitors, in addition to the nests, also their food sources, and the lowest level by submissive species, which defend only their nests and yield to stronger competitors in all other conflict situations.

The higher the ant species' position in the hierarchy, the stronger its impact on species with lower hierarchic status. As a rule, territorials exclude each other and significantly limit the nesting ability of encounterers (Hölldobler and Wilson, 1977; Savolainen and Vepsäläinen, 1988; Savolainen et al., 1989; Markó and Czechowski, 2004; Cerdá et al., 2013; Czechowski et al., 2013; Markó et al., 2013; Ślipiński et al., 2014; Adams, 2016). The possibility of co-occurrence of different ant species is also context-dependent, determined by several other factors like climatic conditions, habitat structure, distribution and properties of food sources, the presence of parasites and predators, etc. (Davidson, 1977; Vepsäläinen, 1978; Levings and Traniello, 1981; Savolainen et al., 1989; Savolainen and Vepsäläinen, 1989; Markó and Czechowski, 2004; Czechowski and Vepsäläinen, 2009; Gibb, 2011;

* Corresponding author. Department of Ecology, University of Szeged, Közép fasor 52, H-6726, Szeged, Hungary.

E-mail addresses: maak.istvan.elek@bio.u-szeged.hu, bikmakk@gmail.com (I.E. Maák).

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Cerdá et al., 2013; Czechowski et al., 2013; Adams, 2016; Stuble et al., 2017).

Competition unavoidably occurs when the ecological requirements of species overlap (Pianka, 1974; Glen and Dickman, 2008). The negative effects of competitive interactions can be weakened if the morphological adaptations and/or behavioural and ecological plasticity of the competing partners allow shifts in their needs, thus reducing niche overlap, which is observed also in ants (see Cerdá et al., 2013 for a review). On the other hand, in ants, the most effective strategy to ensure the control of resources, and thus an advantage over competitors is territoriality (Hölldobler and Wilson, 1990; Adams, 2016). Territorial ants dominate their foraging areas, exerting stronger or weaker pressure on the cohabiting ant species (Savolainen and Vepsäläinen, 1988); in general, the more competitive a species to a dominant, the further the former can nest from the latter (Savolainen and Vepsäläinen 1988, 1989; Czechowski et al., 2013; Adams, 2016; Trigos-Peral et al., 2016; Ślipiński et al., 2018).

Clear division of food resources contributes to the decrease in competitive pressure (Levings and Traniello, 1981; Sorvari and Hakkarainen, 2004). The cohabitation of two morphologically similar species can be ensured by behavioural differences: while a species can dominate in contest competition due to its aggressive behaviour, the other can adjust its foraging strategy by being faster in retrieving the prey and/or more efficient in discovering food supplies (Reznikova, 1982; Savolainen, 1991; Gordon, 2010). Under stable circumstances, a lower-ranked species can cohabit with a species of a higher level, but when supplies diminish, the competition between them increases to a degree that prevents further coexistence (Savolainen and Vepsäläinen, 1988; Markó and Czechowski, 2004; Cerdá et al., 2013; Czechowski et al., 2013; Markó et al., 2013; Ślipiński et al., 2014).

The North-Palaearctic (including boreo-montane) species of the *Formica rufa* group are highly aggressive territorial ants that can often develop multi-nest polydomous systems (interrelated nests formed by colony fissions), with possible worker, queen, brood and information exchange in-between (Czechowski et al., 2012; Stockan and Robinson, 2016; Seifert, 2018). In temperate forest ecosystems, wood ants of the *F. rufa* group are the most common top dominants of the ant communities, which makes them the main structuring factor for these communities; they have a strong influence on the composition, distribution and density of other ant species (Savolainen et al., 1989; Savolainen et al., 1989; Czechowski and Vepsäläinen, 2001; Czechowski and Markó, 2006; Väänänen et al., 2010; Stukalyuk, 2015) and can lower their fitness and modify their activity and foraging habits (Savolainen, 1990, 1991; Czechowski and Markó, 2005). Within their territory, they usually exclude other strong competitors, but the submissive species can occur in quite high density (Savolainen and Vepsäläinen, 1989; Czechowski and Markó, 2005; Väänänen et al., 2010; Stukalyuk, 2015; Seifert, 2018). Along with the increasing distance from their nests, the abundance of other species may increase proportionally (Savolainen and Vepsäläinen, 1989). Despite fairly large knowledge about the competitive effect of the territorial wood ants on other ant species, there is still a lack of a detailed comparison of the impact of colonies of different wood ants species on the nesting habits of their subordinates (encounterers and submissives).

In this study, we investigated the small-scale effect of two wood ant species of the *F. rufa* group, namely *F. rufa* and *F. polyctena*, on local communities of the subordinate ant species. We hypothesized that the differences in the characteristics of each of these two territorials (see below) will be reflected in the patterns of occurrence of the subordinates, especially submissive species that can be more than encounterers tolerated by wood ants in close vicinity of the mounds of the latter. We expected the nest density of the submissives to be negatively correlated with the mound size (as a relative measure of the wood ant colony size). The difference in the mound size will be reflected in the different activity of wood ant workers within their territory, which in turn will influence the density of nests of other species. We also expected

that the increasing distance from the wood ants' mounds will have a positive effect on the nest density of the subordinate, mostly encounter species, as the impact of wood ants on these species is expected to be higher than on the submissives.

2. Material and methods

2.1. Study species

Formica rufa Linnaeus 1761 and *F. polyctena* Förster 1850 are North-Palaearctic oligotopes (species occurring in habitats of a few similar types, or species that demand a specific physical habitat factor, irrespective of the general type of vegetation, see Czechowski et al., 2012) of temperate and sub-mountain coniferous and mixed forests, met also in deciduous forests (Czechowski et al., 2012; Seifert, 2018). Both *F. rufa* and *F. polyctena*, as fairly thermophilic species, they occur mainly in sunny places, on glades, forest edges and along forest roads, although they are also found in shady places deep in the forest (*F. rufa* less often, *F. polyctena* more often). They build nests with impressive mounds of dry plant particles (coarser in *F. rufa*, finer in *F. polyctena*); in *F. rufa*, the diameter of the mound may exceed 1 m, in *F. polyctena*, even 3 m (Czechowski et al., 2012; Seifert, 2018). Like all wood ants, they forage in all forest layers, from the roots, through the ground to tree canopies, as honeydew collectors, scavengers and non-selective predators against a variety of invertebrates. Having similar habitat requirements and biology, these two species differ in structure and social organization. Colonies of *F. rufa* in continental Eurasia are usually monogynous, i.e. one-queened (in the British Isles, they are usually polygynous), and thus monodomous; their sizes reach several hundred thousand workers. In contrast, colonies of *F. polyctena* (absent from the British Isles) are generally highly polygynous (up to a few thousand queens in one nest), and frequently number over a million workers. Due to polygyny, they often form extensive multi-nest (polydomous) systems (Collingwood, 1979; Czechowski et al., 2012; Seifert, 2018).

2.2. Study area and sampling design

We carried out the fieldwork in the managed part of the Białowieża Forest (52°41.891'N, 23°53.477'E; N-E Poland) near the border with Belarus in July 2017. The tree stands of the studied mixed forest consisted mainly of the pedunculate oak (*Quercus robur*), Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), silver birch (*Betula pendula*) and hornbeam (*Carpinus betulus*) (Sokołowski, 2004). The age of the pine and spruce trees varies between 32 and 180 years (Forest Data Bank). The annual mean air temperature and precipitation are 6.8 °C and 633 mm, respectively (Pierzgalski et al., 2002). Fawn-brown podzolized soil and different types of rusty brown forest soils are representative for the area (Forest Data Bank).

For the purpose of the study, we selected 10 individual colonies of each of the considered wood ant species. Each of them was located more than 200 m from the nearest (co- or allospecific) other wood ant mound. The mound volume above ground level was determined using the formula for the volume of half ellipsoid:

$$V = (0.75 * \pi * r_1 * r_2 * h) / \quad (2)$$

were h being the height of the mound, and r_1 and r_2 are the two perpendicular nest radii. It is recognized that the above-ground mound volume correlates with the wood ant colony size (Punttila and Kilpeläinen, 2009; Risch et al., 2005).

Around each of the selected wood ant mounds, we marked out four transects in the directions S, W, N and E. On each of the transects, we established three square plots with an area of 10 m² (approx. 3.16 × 3.16 m); a total of 12 plots per mound, at 10, 20 and 30 m from the mound. The distance was measured from the edge of the mound to the centre of the given quadrat. Within every plot, we mapped the number

of ant nests, their exact location within the quadrat and their distance from each other, and the presence of wood ant workers (foraging trails or dispersed individuals). If the latter were present, we considered that plot with high wood ant presence (WA+), whereas when no wood ants were found, that plot was considered with low wood ant presence (WA-). A sample for species identification was taken from each found nest. Ants, both those of the subordinate species and (earlier) of the wood ant species were identified by using the keys of Seifert (2007) and Czechowski et al. (2012). Voucher specimens are deposited in the Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw.

2.3. Data analysis

The total number of subordinate ant nests per species found within the territories of *F. rufa* and *F. polyctena* were compared with paired Wilcoxon test ($N = 13$). We also calculated the Shannon Wiener entropies for the territories of each of the two wood ant species based on the total number of subordinate ant nests of different species.

To compare the sizes of the mounds of each of the two wood ant species we used a general linear model (GLM, Gaussian error, maximum likelihood fit). In the model, the species ID was included as an explanatory factor ($N = 20$). The effect of the mound size, the wood ant species and their interaction on the total number of subordinate ant nests within the wood ant territories were also analysed with GLM (Gaussian error, maximum likelihood fit, $N = 20$). In the model, the species ID was included as an explanatory factor, whereas the wood ant mound size and their interaction as covariates.

The effect of the wood ant species (*F. rufa* and *F. polyctena*), the distance from the wood ant mound and the wood ant worker presence within the plots (WA-, WA+) on the number of nests found within the plots was tested with GLMM (Poisson error, maximum likelihood fit, $N = 240$). In the model, the wood ant species, the wood ant worker presence (WA-/WA+), the distance and the interaction of the two latter were included as explanatory factors, whereas the nest mound ID was included as a random factor ($N = 240$). Separate models were built for the number of all the nests found within the study plots, of the nests belonging to the genus *Myrmica*, of the nests of other species than those of the genus *Myrmica*, and of the nests of each of the two most abundant *Myrmica* species, i.e. *M. rubra* and *M. ruginodis*. The same model construction (GLMM, Poisson error, maximum likelihood fit, $N = 240$) was used to test the effect of the wood ant species, the wood ant worker presence (WA-/WA+), the distance from the wood ant mound and the interaction of the two latter on the number of ant species found in the different plots. The best models were selected with automated model selection.

The relationship between the total number of nests found in plots at different distances (10, 20, 30 m) and directions (S, W, N, E) from the wood ant mounds was analysed using the χ^2 test. The total number of nests found in the different plots were summed up according to the different distances and directions.

If necessary, the variables were log-transformed prior to the analyses to meet the normality and homogeneity of variances. In model overdispersion, a negative binomial error structure was applied (see Lindén and Mäntyniemi, 2011). Statistical analyses were carried out in R Statistical Environment (R Core Team, 2019). GLMs were performed using the 'glm' function, whereas χ^2 analysis was performed using the 'chisq.test' function from the Stats package. GLMMs were performed using the 'glmer' function from the lme4 package (Bates et al., 2013). Automated model selection was carried out with the help of the dredge function in the MuMIn package (Bartoń, 2019). The 'emmeans' function (emmeans package) was used for sequential post-hoc comparisons among factor levels when performing GLMM analyses (Russell, 2019).

3. Results

Altogether, within the territories of the two wood ant species, there

were 554 nests of 13 subordinate ant species in the plots studied (Table 1). In the *F. rufa* territories, 90.40% and in the *F. polyctena* territories, 90.48% of these nests belonged to two *Myrmica* species: *M. rubra* and *M. ruginodis* (Table 1). Only 53 nests (9.56%), 29 in *F. rufa* and 24 in *F. polyctena*, represented other species than these two (Table 1). There was no significant difference between the number of nests in the territories of each of the wood ant (paired Wilcoxon $V = 31$, $p = 0.32$). Also, the Shannon Wiener entropy index calculated based on the number of nests of the subordinate species was the same for *F. rufa* and *F. polyctena* ($H = 0.96$ in both cases).

The number of subordinate species and the number of their nests had an even distribution along with the distance from the wood ant mounds (Table 1). Plots with the highest number of species (4) and the highest number of nests (9) were found at every distance considered. The average nest density was only slightly larger in WA- ($0.274/\text{m}^2$) and larger in WA+ ($0.234/\text{m}^2$) plots in *F. rufa* than in *F. polyctena* (WA-: $0.264/\text{m}^2$, WA+: $0.197/\text{m}^2$). However, in both species, the nest density was slightly larger in plots with lower wood ant presence (WA-) than in ones with higher presence (WA+) (Fig. 1). Nests of the encounter species of the genus *Lasius* (except the underground *L. flavus*) were present in 5.63% and 4.37% of the total nests in *F. rufa* and *F. polyctena*, respectively (Table 1). The most abundant species of this genus, *L. platythorax*, had its nests quite evenly distributed along with the distances (Table 1). Only one nest of other encounter species, *Camponotus herculeanus*, was found at 10 m distance from a mound of *F. rufa*, and a few workers from a nearby nest outside a studied plot were also seen at a distance of 20 and 30 m. We found only two nests of subordinate *Formica* species (*F. fusca*) within one of the *F. polyctena* territories (at a distance of 30 m from the mound) (Table 1). However, individual workers were also seen at 10 m and 20 m from the mounds of *F. rufa* and *F. polyctena*, respectively.

Mound volumes (in dm^3) of the studied nests of *F. rufa* (427.79 ± 359.95 , mean \pm SD) were significantly smaller than those of *F. polyctena* (1465.45 ± 747.28 , mean \pm SD; GLM $t = -4.3$, $p < 0.001$). However, the wood ant species (GLM $t = 0.34$, $p = 0.74$), their mound size ($t = 1.25$, $p = 0.23$) and the interaction of the two ($z = -1.27$, $p = 0.2$) did not have any effect of the total number of nests within their territory (Fig. 2).

We found 50 (41.66%) plots with low wood ant presence (WA-) in *F. rufa* and 25 (20.83%) ones in *F. polyctena*, which resulted in 46 more nests of subordinate species within the territories of *F. rufa* (Table 1, S1). Based on the variables retained in the best models, the wood ant presence affected negatively the number of all nests and marginally the number of all *Myrmica* nests within the plots (Table 2). Such an effect could be observed on the number of *M. rubra* nests, but not in the

Table 1

The number of nests belonging to different subordinate ant species found on the territories of the two wood ants (*F. rufa* and *F. polyctena*) at different distances from the mounds, their total numbers depending on the wood ant species and the total number of nests found in different subordinate species.

Species	10 m	20 m	30 m	<i>F. rufa</i>	<i>F. polyctena</i>	Total
<i>Camponotus herculeanus</i>	1	0	0	1	0	1
<i>Formica fusca</i>	0	0	2	0	2	2
<i>Lasius brunneus</i>	0	1	0	1	0	1
<i>Lasius flavus</i>	0	0	1	1	0	1
<i>Lasius niger</i>	2	0	1	3	0	3
<i>Lasius platythorax</i>	6	6	12	13	11	24
<i>Myrmica lobicornis</i>	0	1	0	0	1	1
<i>Myrmica lonae</i>	1	1	6	3	5	8
<i>Myrmica rubra</i>	39	32	45	57	59	116
<i>Myrmica ruginodis</i>	132	134	119	216	169	385
<i>Stenamma debile</i>	4	1	2	1	6	7
<i>Tennothorax corticalis</i>	0	1	0	1	0	1
<i>Tennothorax crassispinus</i>	1	3	0	3	1	4
Total number of nests	186	180	188	300	254	554
Total number of species	8	9	8	12	8	13

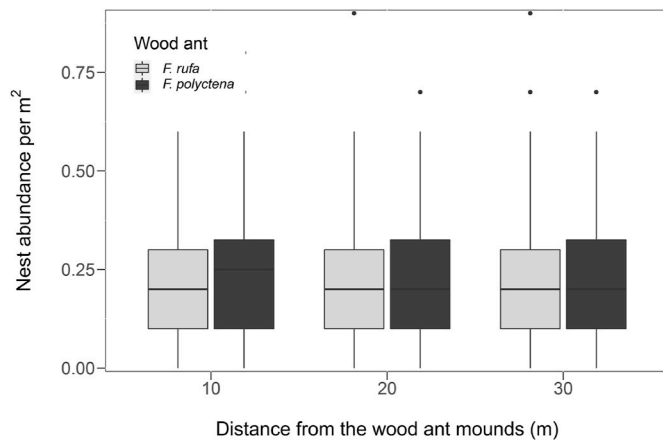


Fig. 1. The nest density of all the subordinate ant species found within the territories of *F. polyctena* (dark grey) and *F. rufa* (light grey) in the plots at different distances from the mounds (medians, quartiles, min-max values and outliers).

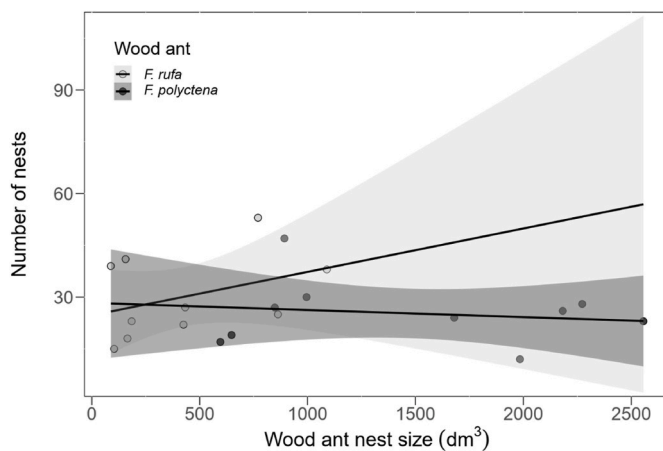


Fig. 2. The effect of the mound size of the wood ant species on the total number of the nests of the subordinate ant species registered in the plots within the territories of the two wood ant species *F. rufa* (light grey) and *F. polyctena* (dark grey). The black lines with confidence bands (grey) are plotted based on the linear regression of the two variables.

Table 2

The effect of different variables on the number of nests (all nests, all *Myrmica* nests, nests belonging to species other than *Myrmica*, *M. rubra*, *M. ruginodis*) found around the mounds of the two wood ant species (*F. rufa* and *F. polyctena*). Only the variables retained in the best models are shown. Significant differences are indicated by bold *P* values.

Model	Variable	z	P
No. of all nests	RWA- vs. RWA+	-2.24	0.025
No. of all <i>Myrmica</i> nests	RWA- vs. RWA+	-1.93	0.054
No. of all other than <i>Myrmica</i> nests	RWA-: 10 m vs. 20 m	0.6	0.818
	RWA-: 10 m vs. 30 m	-0.98	0.593
	RWA-: 20 m vs. 30 m	-2.16	0.078
	RWA+: 10 m vs. 20 m	-2.08	0.094
	RWA+: 10 m vs. 30 m	1.54	0.272
	RWA+: 20 m vs. 30 m	2.71	0.018
	10 m: RWA- vs. RWA+	-0.97	0.332
20 m: RWA- vs. RWA+	-3.08	0.002	
30 m: RWA- vs. RWA+	1.34	0.179	
No. of <i>M. rubra</i> nests	RWA- vs. RWA+	-2.64	0.008
No. of <i>M. ruginodis</i> nests	FORU vs. FOPO	1.18	0.238

M. ruginodis, or other species than those of the *Myrmica* genus (Table 2). In the latter, however, the wood ant presence had a negative effect only in the plots at 20 m (Table 2). Moreover, in the plots with higher wood ant presence (WA+), the number of nests was significantly higher in the plots at 30 m than at 20 m (Table 2). The distance from the mounds and wood ant activity did not have any other significant effects (Table 2). The wood ant species did not have a significant effect on the number of *M. ruginodis* nests (Table 2). Considering the total number of nests within plots, we did not find any relationship between plot distance and their direction (Chi2 = 7.07, p = 0.31).

The only variable included in the best model analysing the number of ant species within the different plots was the wood ant presence (WA-/WA+) that did not have a significant effect (GLMM z = -1.57, p = 0.12).

4. Discussion

We studied the small-scale effect of two territorial wood ant species on the occurrence of subordinate ants in the vicinity of their mounds. The smaller mound sizes found in *F. rufa* than those in *F. polyctena* were in concordance with a generally lower density of this species on its territory than that of the latter, however, this did not cause a difference in the nest number of other ant species within the compared wood ants' territories. Intensity of the negative effect of wood ant activity on the nest density of the subordinate species within the studied plots was species-dependent. Moreover, the distribution of the nests of these species was only slightly influenced by the distance from the wood ant mounds even in plots with high wood ant presence.

The two wood ant species showed a clear difference in the mound size within the studied habitat, which might be linked to the monogynous or polygynous nature of the colonies of these species. Considering also these differences between the two species, like the common monogyny in *F. rufa* vs. high polygyny in *F. polyctena* (Czechowski et al., 2012; Seifert, 2018), their differential effect on nest density of the subordinate species would be expected. However, we did not find any significant difference regarding the diversity and abundance of other, mostly submissive ant species. Considering the smaller nest (= colony) sizes in *F. rufa*, this lack of differences can signal somehow a stronger effect of this species on other ants than that of *F. polyctena*. This may be associated with the diverse aggressiveness of workers of the territorial *Formica* species, decreasing in a gradient from monogynous-monodomous to polygynous-polydomous colonies (Pisarski 1973, 1982; Mabelis, 2003).

Considering strictly the nest density, it seems that in plots with higher ant activity, *F. rufa* workers had a lower effect on the number of nests of other ant species. These values (*F. rufa* WA+: 0.234/m², *F. polyctena* WA+: 0.197/m²) were lower than those found in pine forest with high *F. polyctena* density (0.376/m²), but higher than the values for similar forest patches without wood ants (0.141/m²) in the Kampinos National Park, Central Poland (Gallé et al., 1998). The more northern patches of open pine forest (Tvärminne, S Finland) without herb layer or with a well-structured herb layer, both without wood ants, had similar nest densities (0.22/m² and 0.18/m², respectively; Gallé et al. 2011) as in our case. Moreover, we found a much lower diversity than those found in the Kampinos National Park (2.19/m² without and 1.57/m² with *F. polyctena*) and in Tvärminne pine forests without wood ants (2.5/m²) (Gallé, 1991; Gallé et al., 1998). On the one hand, the low values found in our case can be due to the relatively close location of the study plots in relation to the wood ant mounds (10–30 m), which was not the case of the referred studies. Moreover, this is supported also by the findings of Czechowski et al. (1995) in the Białowieża Forest (in the other studied region of the forest than ours), where, in mature moist pine forests, practically without the wood ants, there were 15 ant species (with the most abundant in terms of the nest numbers *M. ruginodis* – 65% and *Leptothorax acervorum* – 16%) and a total nest density was 0.430/m². However, in other mature moist pine forests, the same authors found nest densities similar to ours (Biała Forest: 13 species, 0.286/m²; Tucholskie Forests: 8 species, 0.224/m²; Czechowski et al.,

1995).

Another possible explanation for the lower ant species richness found in the older stands dominated by wood ants (what results from their life history; see Pisarski and Czechowski, 1994) can be related to habitat characteristics, like the herb layer, soil type or other conditions in these stands that allow the adaptation for only a few ant species, and in such situations, even the removal of the dominant wood ants can have no effect on other species (Gibb and Johansson, 2010; Johansson and Gibb, 2016). On the other hand, the relatively high ant abundance values found in the older tree stands in the presence of wood ants (both in our study and in the Kampinos National Park; Gallé et al., 1998), might be due to the indirect positive effects of wood ants on some of the ant species, like the shelter offered for some submissives (Savolainen and Vepsäläinen, 1989; Czechowski and Vepsäläinen, 2001; Czechowski and Markó, 2006; Väänänen et al., 2010; Stukalyuk, 2015). In addition, other ant species nesting within wood ants' territories may also use small food items left behind by wood ant foragers or honeydew falling on the ground during its exploitation (Dixon, 2005; Seeger and Filser, 2008). Such waste can be important food sources in relatively poor habitats.

We found a negative effect of the wood ant activity on the distribution of some subordinate ant species, mostly *M. rubra*. However, no such effect was detected on the *M. ruginodis* and encounter species (i.e. those of the genera *Lasius* and *Camponotus*), which had a quite even distribution along the growing distance from the wood ant mounds. This is contrary to the clear negative effects of *F. polyctena* found in Finland (Savolainen and Vepsäläinen, 1989). This difference can be caused by various factors. On the one hand, the availability of the wood ants' food sources is much higher in the southern than northern regions, which mostly concerns the main source, namely honeydew (Johansson and Gibb, 2016). Generally, a seasonality is found in the food demand of wood ant colonies, with a food shortage leading to higher competition and strong territoriality in the spring and lower demand in the mid-summer period (June–July) after flying out (nuptial flights usually occur in May to June; Czechowski et al., 2012; Seifert, 2018) of the sexuals (Hölldobler and Lumsden, 1980). In the latter period, wood ants defend only specific resources (aphid colonies) within their home range (Hölldobler and Lumsden, 1980). This can lead to lower pressure on other ant species living in the neighbourhood of wood ant mounds in this period (Johansson and Gibb, 2016). However, this can change in the late summer and autumn, when the high protein demand of the brood can lead to an increase in prey retrieval (Rosengren, 1977). On the other hand, the most abundant ant species within the wood ant territories were two species of the genus *Myrmica*. They differ from wood ants in many respects: morphologically, behaviourally, they have different foraging strategy, periods of activity, a way of the area splitting, etc. (Savolainen and Vepsäläinen, 1989). Their workers can escape conflicts close to a wood ant mound by shifting from surface activity to the litter (Savolainen and Vepsäläinen, 1988, 1989; Savolainen, 1990), but they are also capable to survive in small patches with small colonies that they can move easily if disturbed (Savolainen and Vepsäläinen, 1989; Vepsäläinen and Savolainen, 1990; Banschbach and Herbers, 1999). In addition, though these two species, *M. rubra* and *M. ruginodis*, differ morphologically and also their ecological requirements overlap (Mabelis, 1977; Alvarado and Gallé, 2000; Vepsäläinen et al., 2000; Czechowski et al., 2012). Although the negative relationship and nest displacement between these two *Myrmica* species can be high (Mabelis, 1977; Elmes, 1991; Markó et al., 2004), we found them next to each other in several plots. The more pronounced negative impact of wood ant activity on *M. rubra*, which has usually larger colonies (Elmes, 1991), is in concordance with the more aggressive nature of this species. On the other hand, *M. ruginodis* shows two social forms: the polygynous microgyna form, which is specialized in changing habitats, and the monogynous macrogyna form, which is specialized in stable climax habitats that can be dominated by wood ants (Seppä and Walin, 1996). This second form is able to coexist with wood ants (Seppä and Walin,

1996), which seems to be the situation of our findings.

Similarly to *M. ruginodis*, the wood ant activity did not have a significant effect on the distribution of the other subordinate species (both encounterers and submissives), although the number of their nests was generally quite low. However, there were more plots with low wood ant presence in *F. rufa* than in *F. polyctena*, and this did not lead to any significant difference in the number of subordinate species, their nest densities and diversity (except *Myrmica* spp.) found in plots with low wood ant presence. Submissive species may display special adaptations to life in the territories of dominant species which help them to survive in the neighbourhood of their colonies (Savolainen and Vepsäläinen, 1988; Vepsäläinen and Savolainen, 1990; Savolainen, 1991; Czechowski and Vepsäläinen, 1999; Erős et al., 2020). Encounter species, in turn, usually establish their colonies close to the territory borders, as far as possible from the nests of dominants, where foraging activity of the latter is relatively low (Rosengren, 1986; Savolainen and Vepsäläinen, 1988, 1989; Savolainen, 1990; Markó and Czechowski, 2004, 2012; Johansson and Gibb, 2016). Moreover, as with submissives, alternative foraging strategies of these species also increase their chances of successful coexisting with the dominant wood ants (Johansson and Gibb, 2016). For example, *Camponotus* species usually forage individually, without special attention from a stronger competitor. In turn, encounter *Lasius* species tend to forage underground, attending root aphids or building protective earth shelters around aphids on plant stems (Czechowski et al., 2011; Johansson and Gibb, 2016; Seifert, 2018). All these adaptations allow the occurrence of various subordinate species, even with reduced colony size and low reproduction rate within territories of the top dominants of the interspecific competition ant hierarchy (Rosengren, 1986; Savolainen and Vepsäläinen, 1988, 1989; Pisarski and Vepsäläinen 1989; Savolainen et al., 1989; Savolainen, 1990, 1991; Vepsäläinen and Savolainen, 1990; Gallé et al., 1998; Czechowski and Vepsäläinen, 1999; Trigoso-Peral et al., 2020).

Despite the clear negative effects, the nests of some encounter (i.e. of the genera *Camponotus* and *Lasius*) and submissive species were found quite close to the wood ant mounds, as observed also in other studies (Czechowski et al., 2013; Maák et al., 2020). Moreover, the activity of wood ants did not force these species strictly in low activity patches and the nest density of subordinates at 10 m from the mound was similar to that at 30 m. These species might take advantage of the presence of wood ants and lower species richness close-by the wood ant mounds also in other ways due to the possibility to change their foraging behaviour (e.g. Johansson and Gibb, 2016). They can also switch to the use of alternative food sources, like the pollen mentioned above, or corpses of wood ants present in high abundance (Czechowski, 2008; Gibb, 2011), scattered through necrophoresis on the forest floor or taken out to the edge of the home range of wood ants forming linear piles (Dluszkij, 1967; Czechowski, 1976). Moreover, foreign ant corpses can be used even as a typical food source by several ant species (Marikovskiy, 1963; Howard and Tschinkel, 1976; Mori et al., 2000). Such resources, although not sufficient to reach normal colony size and reproduction (see Rutkowski et al., 2019), but – by flexibly adapting the life strategy to the current environmental conditions – may allow the colonies to survive while maintaining relatively large nest densities. In this light, our results support the context-dependent effect of the territorial ants on other ant species (see Adams, 2016; Johansson and Gibb, 2016; Stuble et al., 2017; Trigoso-Peral et al., 2020).

Author contributions

I.M., I.S. and W.Cz. conceived and designed the study; I.M., I.S., O.J., A.T. and J.C. performed field surveys and collected the data; G.T.P. identified the ants; I.M. and O.J. analysed the data; I.M., G.T.P., W.Cz. prepared the figures, and wrote the manuscript. All the authors reviewed and approved the manuscript.

Data availability

The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.actao.2021.103709>.

References

- Adams, E.S., 2016. Territoriality in ants (Hymenoptera: Formicidae): a review. *Myrmecol. News* 23, 101–118.
- Adler, F.R., Lebrun, E.G., Feener Jr., D.H., 2007. Maintaining diversity in an ant community: modeling, extending, and testing the dominance discovery trade off. *Am. Nat.* 169, 323–333. <https://doi.org/10.1086/510759>.
- Alvarado, M., Gallé, L., 2000. Ant assemblages associated with lowland forests in the southern part of the Great Hungarian Plain. *Acta Zool. Hung.* 46, 79–102.
- Bansbach, V.S., Herbers, J.M., 1999. Nest movements and population spatial structure of the forest ant *Myrmica punctiventris* (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am.* 92, 414–423.
- Bartoń, K., 2019. MuMIn: Multi-Model Inference. R package version 1.43.6. <http://CRAN.R-project.org/package=MuMIn>. (Accessed 29 October 2013). published online.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2013. lme4: Linear Mixed-Effects Models Using Eigen and S4. R Package Version 1.0-5. <http://CRAN.R-project.org/package=lme4>. (Accessed 25 October 2013). published online.
- Braschler, B., Baur, B., 2003. Effects of experimental small-scale grassland fragmentation on spatial distribution, density, and persistence of ant nests. *Ecol. Entomol.* 28, 651–658. <https://doi.org/10.1111/j.1365-2311.2003.00549.x>.
- Cerda, X., Arnan, X., Retana, J., 2013. Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology. *Myrmecol. News* 18, 131–147.
- Collingwood, C.A., 1979. The Formicidae (Hymenoptera) of Fennoscandia and Denmark. *Fauna Entomol. Scand.* 8, 1–174.
- Czechowski, W., 1976. Ants cemeteries. *Przegląd Zool.* 20, 417–427 [in Polish with English summary].
- Czechowski, W., 2008. Around nest cemeteries of *Myrmica schencki* Em. (Hymenoptera: Formicidae): their origin and a possible significance. *Pol. J. Ecol.* 56, 359–363.
- Czechowski, W., Vepsäläinen, K., 1999. Plesio-biosis between *Formica fusca* L. and *Formica aquilonia* Yarr. (Hymenoptera, Formicidae). *Ann. Zool.* 49, 125–127.
- Czechowski, W., Vepsäläinen, K., 2001. *Formica rufa* protects indirectly *F. fusca* against raids of *F. sanguinea*. *Ann. Zool.* 51, 267–273.
- Czechowski, W., Markó, B., 2005. Competition between *Formica cinerea* Mayr (Hymenoptera: Formicidae) and co-occurring ant species, with special reference to *Formica rufa* L.: direct and indirect interferences. *Pol. J. Ecol.* 53, 467–487.
- Czechowski, W., Markó, B., 2006. Uncomfortable protection: *Formica polyctena* Först. shelters *Formica fusca* L. from *Formica sanguinea* Latr. (Hymenoptera: Formicidae). *Ann. Zool.* 56, 539–548. <https://doi.org/10.3161/000345406778811808>.
- Czechowski, W., Vepsäläinen, K., 2009. Territory size of wood ants (Hymenoptera: Formicidae): a search for limits of existence of *Formica polyctena* Först., an inherently polygynic and polycalic species. *Ann. Zool.* 59, 179–187. <https://doi.org/10.3161/000345409X463994>.
- Czechowski, W., Pisarski, B., Yamauchi, K., 1995. Succession of ant communities (Hymenoptera, Formicidae) in moist pine forests. *Fragm. Faun. (Wars.)* 38, 447–488.
- Czechowski, W., Markó, B., Erős, K., Csata, E., 2011. Pollenivory in ants (Hymenoptera: Formicidae) seems to be much more common than it was thought. *Ann. Zool.* 61, 519–525.
- Czechowski, W., Radchenko, A., Czechowska, W., Vepsäläinen, K., 2012. The Ants of Poland with Reference to the Myrmecofauna of Europe. *Fauna Poloniae* 4. Natura Optima Dux Foundation, Warszawa, Poland, pp. 189–205.
- Czechowski, W., Markó, B., Radchenko, A., Ślipiński, P., 2013. Long-term partitioning of space between two territorial species of ants (Hymenoptera: Formicidae) and their effect on subordinate species. *Eur. J. Entomol.* 110, 327–337.
- Davidson, D., 1977. Species diversity and community organization in desert seed-eating ants. *Ecology* 58, 711–724. <https://doi.org/10.2307/1936208>.
- Dixon, T., 2005. Insect Herbivore – Host Dynamics. *Tree-dwelling aphids*. Cambridge University Press, Cambridge.
- Blusskij, G.M., 1967. Ants of the genus *Formica* (Hymenoptera, Formicidae, g. *Formica*). Nauka, Moskva, p. 236 [in Russian].
- Elmes, G.W., 1991. The social biology of *Myrmica* ants. *Actes Coll. Insect. Soc.* 7, 17–34.
- Erős, K., Maák, I., Markó, B., Babik, H., Ślipiński, P., Nicoară, R., Czechowski, W., 2020. Competitive pressure by territorial ants promotes utilization of unusual food source by subordinate ants in temperate European woodlands. *Ethol. Ecol. Evol.* 32, 457–465. <https://doi.org/10.1080/03949370.2020.1753116>.
- Forest Data Bank. Bank Danych o Lasach. <https://www.bdl.lasy.gov.pl/portal/mapy-en> (Accessed 28 June 2020).
- Gallé, L., 1991. Structure and succession of ant assemblages in a north European sand dune area. *Holarctic Ecol.* 14, 31–37.
- Gallé, L., Körmöczy, L., Hornung, E., Kerekes, J., 1998. Structure of ant-assemblages in a middle-European successional sand-dune area. *Tiscia* 31, 19–28.
- Gibb, H., 2011. Experimental evidence for mediation of competition by habitat succession. *Ecology* 92, 1871. <https://doi.org/10.1890/10-2363.1>.
- Gibb, H., Johansson, T., 2010. Forest succession and harvesting of hemipteran honeydew by boreal ants. *Ann. Zool. Fenn.* 47, 99–110.
- Glen, A.S., Dickman, C.R., 2008. Niche overlap between marsupial and eutherian carnivores: does competition threaten the endangered spotted-tailed quoll? *J. Appl. Ecol.* 45, 700–707. <https://doi.org/10.1111/j.1365-2664.2007.01449.x>.
- Gordon, D.M., 2010. Ant Encounters: Interaction Networks and Colony Behavior. Princeton University Press, USA.
- Hölldobler, B., Wilson, E.O., 1977. The number of queens: an important trait in ant evolution. *Naturwissenschaften* 64, 8–15. <https://doi.org/10.1007/BF00439886>.
- Hölldobler, B., Lumsden, C.J., 1980. Territorial strategies in ants. *Science* 210, 732–739.
- Hölldobler, B., Wilson, E.O., 1990. The Ants. The Belknap Press of Harvard University Press, Cambridge, USA.
- Howard, D., Tschinkel, W.R., 1976. Aspects of necrophoric behavior in the red imported fire ant, *Solenopsis invicta*. *Behavior* (56), 157–178.
- Johansson, T., Gibb, H., 2016. Interspecific competition and coexistence between wood ants. In: Stockan, J.A., Robinson, E.J. (Eds.), *Wood Ant Ecology and Conservation*. Cambridge University Press, Cambridge, UK, 13: 9781107048331.
- Levings, S., Traniello, J., 1981. Territoriality, nest dispersion, and community structure in ants. *Psyche* 88, 265–319. <https://doi.org/10.1155/1981/20795>.
- Lindén, A., Mäntyniemi, S., 2011. Using the negative binomial distribution to model overdispersion in ecological count data. *Ecology* 97, 1414–1421.
- Maák, I., Czekes, Zs., Erős, K., Pálfi, Zs., Markó, B., 2020. Living on the edge: changes in the foraging strategy of a territorial ant species occurring with a rival supercolony – a case study. *J. Insect Behav.* 33, 59–68.
- Mabelis, A.A., 1977. Artenreichtum von Ameisen in einigen Waldtypen. In: Tüxen, R. (Ed.), *Berichte der Internationalen Symposien der Internationalen Vereinigung für Vegetationskunde*. Vaduz.
- Mabelis, A.A., 2003. Do *Formica* species (Hymenoptera: Formicidae) have a different attack mode? *Ann. Zool.* 53, 667–668.
- Marikovsky, P.I., 1963. The ants *Formica sanguinea* as pillagers of *Formica rufa* Lin. nests. *Insect. Soc.* 10, 119–128.
- Markó, B., Czechowski, W., 2004. *Lasius psammophilus* Seifert and *Formica cinerea* Mayr (Hymenoptera: Formicidae) on sand dunes: conflict and coexistence. *Ann. Zool.* 54, 365–378. <https://doi.org/10.3161/0003454043540909>.
- Markó, B., Czechowski, W., 2012. Space use, foraging success and competitive relationships in *Formica cinerea* (Hymenoptera Formicidae) on sand dunes in southern Finland. *Ethol. Ecol. Evol.* 24, 149–164.
- Markó, B., Kiss, K., Gallé, L., 2004. Mosaic structure of ant communities (Hymenoptera: Formicidae) in eastern Carpathian marshes: regional versus local scales. *Acta Zool. Hung.* 50, 77–95.
- Markó, B., Czechowski, W., Radchenko, A., 2013. Combining competition with predation: drastic effect of *Lasius fuliginosus* (Latr.) on subordinate ant species at the northern limit of its distribution. *Ann. Zool.* 63, 107–111. <https://doi.org/10.3161/000345413X666156>.
- Mori, A., Grasso, D., Le Moli, F., 2000. Raiding and foraging behavior of the blood-red ant, *Formica sanguinea* Latr. (Hymenoptera, Formicidae). *J. Insect Behav.* 13, 421–437.
- Pianka, E.R., 1974. Niche overlap and diffuse competition. *Proc. Natl. Acad. Sci. Unit. States Am.* 71, 2141–2145. <https://doi.org/10.1073/pnas.71.5.2141>.
- Pierzgalski, E., Boczoń, A., Tyszka, J., 2002. Variability of precipitation and ground water level in the Białowieża National Park. *Kosmos* 51, 415–425.
- Pisarski, B., 1973. Social structure of *Formica (Coptoformica) exsecta* Nyl. (Hymenoptera: Formicidae) and its influence on morphology, ecology and ethology of the species. *Zoological Institute PAS, Warszawa*, p. 134 [in Polish].
- Structure et organisation des sociétés de fourmis de l'espèce *Formica (Coptoformica) exsecta* Nyl. (Hymenoptera, Formicidae). In: Pisarski, B. (Ed.), *Memorabilia Zool.* 38, 281.
- Pisarski, B., Vepsäläinen, K., 1989. Competition hierarchies in ant communities (Hymenoptera, Formicidae). *Ann. Zool.* 42, 321–329.
- Pisarski, B., Czechowski, W., 1994. Ways to reproductive success of wood ant queens. *Memorabilia Zool.* 48, 181–186.
- Punttilä, P., Haila, Y., Tukia, H., 1996. Ant communities in taiga clearcuts: habitat effects and species interactions. *Ecography* 19, 16–28. <https://doi.org/10.1111/j.1600-0587.1996.tb00151.x>.

- Punttila, P., Kilpeläinen, J., 2009. Distribution of mound-building ant species (*Formica* spp., Hymenoptera) in Finland: preliminary results of a national survey. *Ann. Zool. Fenn.* 46, 1–15.
- R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from. <http://www.R-project.org/>.
- Reznikova, J.I., 1982. Interspecific communication between ants. *Behaviour* 80, 84–95. <https://doi.org/10.1163/156853982X00454>.
- Risch, A.C., Jurgensen, M.F., Schütz, M., Page-Dumroese, D.S., 2005. The contribution of red wood ants to soil C and N pools and CO₂ emissions in subalpine forests. *Ecology* 86, 419–430.
- Rosengren, R., 1977. Foraging strategy of wood ants (*Formica rufa* group). I. Age polyethism and topographic traditions. *Ann. Zool. Fenn.* 150, 1–30.
- Rosengren, R., 1986. Competition and coexistence in an insular ant community: a manipulation experiment (Hymenoptera: Formicidae). *Ann. Zool. Fenn.* 23, 297–302.
- Russell, L., 2019. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.4.2. <https://CRAN.R-project.org/package=emmeans>.
- Rutkowski, T., Maák, I., Vepsäläinen, K., Trigos-Peral, G., Stephan, W., Wojtaszyn, G., Czechowski, W., 2019. Ants trapped for years in an old bunker; survival by cannibalism and eventual escape. *J. Hymenoptera Res.* 72, 177–184.
- Sanders, N., Gordon, D., 2003. Resource-dependent interactions and the organization of desert ant communities. *Ecology* 84, 1024–1031. [https://doi.org/10.1890/0012-9658\(2003\)084](https://doi.org/10.1890/0012-9658(2003)084).
- Savolainen, R., 1990. Colony success of the submissive ant *Formica fusca* within territories of the dominant *Formica polyctena*. *Ecol. Entomol.* 15, 79–85.
- Savolainen, R., 1991. Interference by wood ant influences size selection and retrieval rate of prey by *Formica fusca*. *Behav. Ecol. Sociobiol.* 28, 1–7. <https://doi.org/10.1007/BF00172132>.
- Savolainen, R., Vepsäläinen, K., 1988. A competition hierarchy among boreal ants: impact on resource partitioning and community structure. *Oikos* 51, 135–155. <https://doi.org/10.2307/3565636>.
- Savolainen, R., Vepsäläinen, K., 1989. Niche differentiation of ant species within territories of the wood ant *Formica polyctena*. *Oikos* 56, 3–16. <https://doi.org/10.2307/3566082>.
- Savolainen, R., Vepsäläinen, K., Wuorenrinne, H., 1989. Ant assemblages in the taiga biome: testing the role of territorial wood ants. *Oekologia* 81, 481–486. <https://doi.org/10.1007/BF00378955>.
- Seeger, J., Filser, J., 2008. Bottom-up down from the top: honeydew as a carbon source for soil organisms. *Eur. J. Soil Biol.* 44, 483–490.
- Seifert, B., 2007. Die Ameisen Mittel- und Nordeuropas. Lutra Verlags- und Vertriebsgesellschaft, Görlitz.
- Seifert, B., 2018. The Ants of Central and North Europe. Lutra Verlags- und Vertriebsgesellschaft, Boxberg, Germany, pp. 318–325.
- Seppä, P., Wallin, L., 1996. Sociogenetic organization of the red ant *Myrmica rubra*. *Behav. Ecol. Sociobiol.* 38, 207–217.
- Sokolowski, A.W., 2004. Lasy Puszczy Białowieskiej. Centrum Informacyjne Lasów Państwowych, Warszawa, Poland.
- Sorvari, J., Hakkarainen, H., 2004. Habitat-related aggressive behaviour between neighbouring colonies of the polydomous wood ant *Formica aquilonia*. *Anim. Behav.* 67, 151–153. <https://doi.org/10.1016/j.anbehav.2003.03.009>.
- Stukalyuk, S.V., 2015. Structure of the ant assemblages (Hymenoptera, Formicidae) in the broad-leaved forests of Kiev. *Entomol. Rev.* 95, 370–387. <https://doi.org/10.1134/S0013873815030094>.
- Stockan, J.A., Robinson, E.J., 2016. Wood Ant Ecology and Conservation. Cambridge University Press, Cambridge, UK, 13: 9781107048331.
- Stuble, K.L., Jurić, I., Cerdá, X., Sanders, N.J., 2017. Dominance hierarchies are a dominant paradigm in ant ecology (Hymenoptera: Formicidae), but should they be? And what is a dominance hierarchy anyways? *Myrmecol. News* 24, 71–81.
- Ślipiński, P., Markó, B., Rzeszowski, K., Babik, H., Czechowski, W., 2014. *Lasius fuliginosus* shapes local ant assemblages. *North-West J. Zool.* 10, 404–412.
- Ślipiński, P., Markó, B., Włodarczyk, T., Czechowski, W., 2018. The foraging strategy of *Formica sanguinea* (Hymenoptera: Formicidae), a facultative slave-maker. *Myrmecol. News* 26, 55–64.
- Trigos-Peral, G., Markó, B., Babik, H., Tausan, I., Maák, I., Pálfi, Zs, Ślipiński, P., Czekes, Zs, Czechowski, W., 2016. Differential impact of two dominant *Formica* ant species (Hymenoptera, Formicidae) on subordinates in temperate Europe. *J. Hymenoptera Res.* 50, 97–116. <https://doi.org/10.3897/JHR.50.8301>.
- Trigos-Peral, G., Rutkowski, T., Witek, M., Ślipiński, P., Babik, H., Czechowski, W., 2020. Three categories of urban green areas and the effect of their different management on the communities of ants, spiders and harvestmen. *Urban Ecosyst.* 23, 803–818.
- Väänänen, S., Vepsäläinen, K., Savolainen, R., 2010. Indirect effects in boreal ant assemblages: territorial wood ants protect potential slaves against enslaving ants. *Ann. Zool.* 60, 57–67. <https://doi.org/10.3161/000345410X499524>.
- Vepsäläinen, K., 1978. Wing dimorphism and diapause in *Gerris*: determination and adaptive significance. In: Dingle, H. (Ed.), *Evolution of Insect Migration and Diapause. Proceedings in Life Sciences*. Springer, New York, USA.
- Vepsäläinen, K., Pisarski, B., 1982. Assembly of island ant communities. *Ann. Zool. Fenn.* 19, 327–335.
- Vepsäläinen, K., Savolainen, R., 1990. The effect of interference by formicine ants on the foraging of *Myrmica*. *J. Anim. Ecol.* 59, 643–654.
- Vepsäläinen, K., Savolainen, R., Tiainen, J., Vilén, J., 2000. Successional changes of ant assemblages after ditching of bogs. *Ann. Zool. Fenn.* 37, 135–149.