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Lasius fuliginosus (Hymenoptera: Formicidae) shapes local ant assemblages

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Abstract. Interspecific competition is a major structuring force in ant assemblages. The assemblages are organized hierarchically, with territorial species as top competitors. In boreal areas and in the temperate deciduous forest biome common territorials are species of the subgenus *Formica* s. str. They are well known for their negative impact on lower-ranked ant species. Less is known, though the structuring role of *Lasius fuliginosus*, another territorial ant species. Some earlier studies have shown or suggested that it may restrictively affect subordinate species (including direct predation toward them) even stronger than wood ants do. In the present study we compared species compositions and nest densities of subordinate ant species within and outside territories of *L. fuliginosus*. The results obtained confirmed that this species visibly impoverishes both qualitatively (reduced species richness, altered dominance structures) and quantitatively (decreased nest densities) ant assemblages within its territories. Furthermore, contrary to what is known in wood ants, there was not detected any noticeable protective effect of *L. fuliginosus* for *Formica fusca* living within the *L. fuliginosus* territory against raids of the slave-maker *Formica sanguinea*. Two colonies of *L. fuliginosus* living under different environmental conditions were studied – one in Finland, and one in Poland.

Key words: community structure, competition hierarchy, *Formica sanguinea*, intraspecific relations, nest density, territoriality.

Introduction

Interspecific competition has an important role in structuring ants' communities (Reznikova 1983, Savolainen & Vepsäläinen 1988, Hölldobler & Wilson 1990, Punttila et al. 1996, Sanders & Gordon 2003, Adler et al. 2007, Cerdá et al. 2013, Czechowski et al. 2013). Palaearctic multi-species ant assemblages – especially well-examined in this respect both in northern temperate deciduous and boreal forest zones (e.g. Pisarski 1980, Vepsäläinen & Pisarski 1982, Pisarski & Vepsäläinen 1989), and southern temperate steppe areas (Reznikova 1980, 1983) – are known to have three-level hierarchical structure, with territorial species constituting the highest tier of the competition hierarchy (Vepsäläinen & Pisarski 1982, Savolainen & Vepsäläinen 1988, Pisarski & Vepsäläinen 1989). Colonies of territorial species defend not only their nests and food sources, but they also defend their whole foraging areas against other territorial colonies (both con- and allospecific). Below them, there are two tiers of subordinated ants: (1) encounter species, which defend their nests and food sources, and (2) submissive species, which defend only their nests. Due to restrictive impact of territorials on occurrence, abundance, foraging possibilities, and reproductive output of subordinates, colonies of territorials are acting as organizing centres of ant assemblages (Savolainen & Vepsäläinen 1988, 1989, Savolainen et al. 1989, Pisarski & Vepsäläinen 1989, Reznikova 1999, Czechowski et al. 2013).

Generally speaking, subordinate ant species are doing worse living within than outside the areas of territorial species. In certain situations, however, nesting 'under the wing' of the top competitor appears to be advantageous for some subordinate species. Thus, members of the subgenus *Serviformica* (e.g. *Formica fusca*) are protected by territorials against slave-making raids of the facultative slave-maker *Formica sanguinea* (Czechowski 1999, 2000a, Czechowski & Vepsäläinen 2001). It may even happen that *Serviformica* populations within such territories of wood ants are significantly more abundant or successful, than outside them (Punttila et al. 1996, Czechowski & Vepsäläinen 2001, Czechowski & Markó 2006, Väänänen et al. 2010).

The vast majority of the data on the role of territorial ant species in structuring ant assemblages in temperate Europe concerns species of the subgenus *Formica* s. str. (e.g. *F. rufa*, *F. polyctena*, *F.*

aquilonia in forests, and *F. pratensis* in grasslands) as top dominants – both in the context of their influence on subordinate species (e.g. Stebaev & Reznikova 1972, de Bruyn 1978, Mabelis 1984, Savolainen 1991, Savolainen & Vepsäläinen 1988, 1989, Pisarski & Vepsäläinen 1989, Savolainen et al. 1989, Vepsäläinen & Savolainen 1990), and their 'protective' effect on potential slave species of *Formica sanguinea* (Punttila et al. 1996, Czechowski & Vepsäläinen 2001, Czechowski & Markó 2006, Väänänen et al. 2010). Incomparably less is known though about a role of other territorial ant species, like *Lasius fuliginosus*. Current data on its influence on the structure of ant assemblages are scarce and mainly vague or episodic. There is no doubt, however, that *L. fuliginosus* is a strongly competitive territorial species, able to successfully compete for area and food sources (e.g. trees with honeydew-providing aphids) with other territorial species including wood ants (Zakharov 1972, Romanova 1975, Mabelis 1984, Czechowski 2000b, Czechowski et al. 2013) and *Liometopum* spp. (Kupyanskaya 1988, Petráková & Schlaghamerský 2011). *Lasius fuliginosus* is also known to be a facultative myrmecophage: it happens to attack colonies of subordinate species and pillage larvae and pupae from their nests (Czechowski 2000b, 2002, Markó et al. 2013). It also interferes during raids of *F. sanguinea* when they violate its territory (Czechowski 1999, 2000a). However, apart from few case studies (e.g. Czechowski et al. 2013), there is not any comprehensive study available on the general features of the effect of this species on local ant assemblages.

The aim of this study was to examine to what extent *L. fuliginosus* is able to shape the ant assemblage within its territory considering in two aspects: (1) the impact on the occurrence and abundance of subordinate species in general, and more specifically (2) the potential 'protective' effect on the abundance of *Serviformica* species threatened by the facultative slave-maker *Formica sanguinea* through inhibition of its raids. A geographically wider approach was applied by including data from Finland and Poland, in order to obtain results that could enable us to formulate more general conclusions regarding the effect of *L. fuliginosus* on northern temperate ant assemblages.

Materials and methods

The study species

Lasius fuliginosus is a Euro-West-Siberian species, a fairly thermophilic oligotope of deciduous forest, encountered also in mixed and coniferous forests. It is a dendrobiont nesting in cavities under the trunk and roots of usually living trees, both deciduous and coniferous; sometimes – after death and decay of the tree – in the ground amongst root remnants. The empty spaces in wood and soil are filled with carton nests of chewed wood particles, glued and impregnated with honeydew and reinforced by hyphae of myrmecophilic fungi. Colonies are very populous with up to two million workers, often polygynous and polycalic. Foragers form distinct narrow trails marked out pheromonally, that lead to aphids on trees and bushes; often these trails partly run in underground tunnels. The ants feed on aphid and coccid honeydew and small insects. In conflict situations they use dendrolasin – a substance produced in their mandibular glands with very strong deterring effect on other ants (Pavan 1959). *Lasius fuliginosus* is an obligate temporary social parasite: young queens start new colonies in nests of species of the subgenus *Chthonolasius* (Seifert 2007, Czechowski et al. 2012).

Colonies studied, sites and field methods

Two fairly large colonies of *L. fuliginosus* living under different environmental conditions were studied – one in Finland (colony F), and one in Poland (colony P). In Finland (site F), the studies were conducted in June 2009 near the village of Tvärminne on Hanko Peninsula (59°50′N, 23°15′E). The colony nested within the vast sand dune complex overgrown with Scotts pine (*Pinus sylvestris*) forest. The same colony F was object of several case studies (Czechowski 1999, 2000a, Czechowski et al. 2011). Colony F nested in and under an old pine stump within a small patch (ca 350 m²) of pine forest on a slope of the sand dune. There was also an auxiliary nest in a willow within this patch. The territory of the colony consisted of the above-mentioned forest patch on the slope and a fragment of a pine forest belt stretching along the foot of the dune. These two parts of the territory, divided with a sandy road, were connected by two *L. fuliginosus* trails crossing the road. The entire hourglass-shaped territory (Fig. 1) was about 1100 m², and included more than 70 trees. The soil was covered with a thick layer of needle litter, cones and dry twigs; in places there were moss and lichen, with patches of heather (*Calluna vulgaris*) here and there. In the vicinity, in a gap in the forest belt, a six-nest complex of *Formica sanguinea* occurred. Apart from these, at least one more *F. sanguinea* colony nested on the other side of the *L. fuliginosus* territory. Individual nests of *F. sanguinea* were situated at a distance of 13 to 47 m from the border of the *L. fuliginosus* territory (Fig. 1). Taking into account raiding behaviour of *F. sanguinea* (see e.g. Mori et al. 2000) and especially a fact that the longest raid observed close to the study locality exceeded 90 m (Czechowski & Radchenko 2006), it means that at least major part of the territory of colony F potentially was within the range of the *F. sanguinea* raids.

In Poland (site P), the study was carried out in June and July 2010 in the Świętokrzyskie Mts, south-west of the town of Skarżysko-Kamienna (51°07′N, 20°51′E). Colony P nested in a birch tree in a subcontinental moist pine forest (*Peucedano-Pinetum*) dominated by Scotts pine with

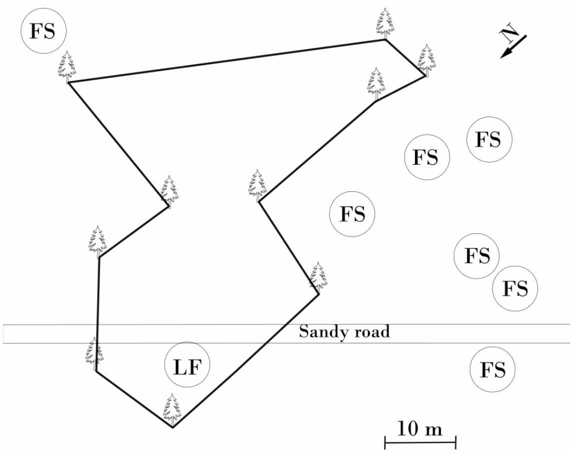

Figure 1. Schematic map of the surroundings of colony F (LF – *L. fuliginosus* nest, FS – *F. sanguinea* nest). Borders of the *L. fuliginosus* territory are sketched basing on the most distant pine trees visited by foragers.

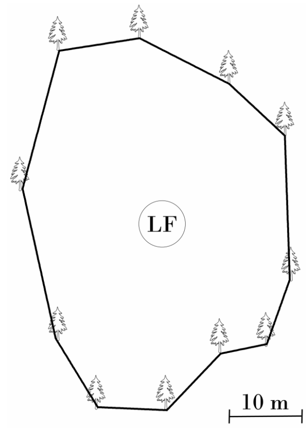

Figure 2. Schematic map of the surroundings of colony P (LF – *L. fuliginosus* nest). Borders of the *L. fuliginosus* territory are sketched basing on the most distant pine trees visited by foragers.

fairly big admixture of birches (*Betula pendula*) and hornbeams (*Carpinus betulus*). The soil was covered with needle litter with the addition of leaves of the deciduous trees; in places there were patches of moss. In herb layer bilberry (*Vaccinium myrtillus*) and cowberry (*V. vitis-idaea*) prevailed. The nest of colony P was centrally situated within the *L. fuliginosus* territory, which was about 1200 m^2 (Fig. 2). No other territorial species (including *Formica sanguinea*) neighboured its territory.

In each study site, within and outside the territory of studied *L. fuliginosus* colonies, occurrence and density of subordinate ants' nests were determined by hand searching of quadrats (biocoenometric frames) of definite sizes: 10 m^2 in Finland (site F), and 1 m^2, 10 m^2 and 100 m^2 in Poland. The quadrats were randomly distributed in each area. In Poland (site P), quadrats were investigated with a searching effort inversely proportional to their size (see Pętal and Pisarski 1966, 1981). Thus, one-square metre quadrats were searched most thoroughly, as these are generally used to detect nests of very small ants which form small colonies and lead cryptic life (e.g. species of the genera *Leptothorax* and *Temnothorax*). Ten-square metre quadrats were searched medium-thoroughly, as this quadrat size is generally used for assessing the abundance of species forming quite numerous colonies and living in relatively easily detectable nests (species of the genera *Myrmica* and *Lasius*). The hundred-square metre quadrats served to estimate most accurately the nest densities of ants of the genera *Formica* and *Camponotus*.

Only quadrats of 10 m^2 were applied in the Finnish site for logistical reasons. However, given its intermediate size, we considered that quadrats of 10 m^2 can still be used to estimate accurately nest densities of species of both small and large colonies. Altogether 54 quadrats were set up at the F study site: 20 within the territory of colony F, 20 quadrats outside the territory in a *L. fuliginosus*-free strip of the forest from the side of the *F. sanguinea* complex, and 14 quadrats were set up in a control area a few hundred meters away, under similar habitat conditions. In this latter case there were no territorial ants in direct proximity, and the area was out of *F. sanguinea* raiding range. The quadrats were searched very carefully, including systematic digging up litter and soil surface in order not to overlook possible small and cryptic nests of *Leptothorax* and *Temnothorax* species (compare methodology for colony P below).

In the Polish study site quadrats were set up within the territory of *L. fuliginosus* colony P and beyond it in a control area of the same habitat conditions situated at 300 m from the territory of colony P. There were no territorial ant species present at the control area. In both areas three size variants of quadrats were used of the same amount: 20 quadrats of 1 m^2, 20 of 10 m^2 and five of 100 m^2. The small number of 100-square metre quadrats resulted from the size limitations of the area of the *L. fuliginosus* territory.

Data management

When different sized-quadrats are used (as for colony P), in the nature of things quadrats are searched with an accuracy inversely proportional to their size. Thereby quadrats of different sizes could deliver different values on the species number and species nest densities. Therefore, in order to obtain accurate values, it is necessary to combine appropriately data received from (Pętal & Pisarski 1966, 1981; see e.g. Czechowski et al. 1995, Babik et al. 2009). Thus, in the case of site P, in order to estimate accurately the nest density of a given species, nest count data were used from quadrats of that size, which were considered to be most adequate for the given species or genus, unless the species was recorded from only one other size quadrat category. Thus, in the case of *Leptothorax* and *Temnothorax* species data from 1 m^2 quadrats were used, for the genera *Myrmica* and *Lasius* those from 10 m² quadrats, and in the case of *Formica* and *Camponotus* nest counts from 100 m² quadrats were used. In each case, nest densities were expressed as number of nests per 100 m².

Generalized Linear Mixed Model (GLMM, Poisson error, Laplace approximation) approach was used to assess the differences in total ant nest number among different area types: *L. fuliginosus*, *Formica sanguinea* and control areas. Site was used as random factor. We used only the nest count data from 10 m² quadrats (n = 75), since these were the common quadrat dataset for the two sites (F and P). The Shannon-Wiener general entropy index (according to the formula based on $\log_{10}$) was used to estimate the diversity of ant assemblages. The index was calculated for all quadrat sizes separately. Redundancy analysis (RDA) based on nest count data from 10 m² quadrats was applied to investigate the relationship between the distribution and abundance of ant species within study sites separately.

GLMM analysis was performed in the R Statistical Environment (R Core Team 2013) using *lme4* package (Bates et al. 2013). *Relevel* function was used in order to carry out post-hoc sequential comparisons among factor levels when performing GLMM, and table-wide sequential Bonferroni-Holm correction was applied to reveal the exact significance levels. PAST 2.17b (Hammer et al. 2001) software was used for the calculation of Shannon-Wiener indices. RDA was performed by the use of CANOCO software (Lepš & Šmilauer 2003).

Results

Species and nest densities

Altogether 54 ant nests of nine subordinate species were found at site F (Table 1). Among these six subordinate ant species were identified from the territory of the *L. fuliginosus* colony, seven species from the area dominated by *Formica sanguinea*, whereas only three species occurred on the control site (Table 1). Total nest density was the highest in the nearby area dominated by *F. sanguinea*, whereas it was lowest in the control area (Table 1). Species compositions of the assemblages were quite similar: the only difference was that *Lasius niger*, an encounter species, was absent from the territory of *L. fuliginosus*. Dominance structures were also similar; however, they differed in the species dominating in respect of nest density (Table 1). The subterranean *Lasius flavus* dominated in this respect within, and *L. niger* outside the territory. The two subdominants, *Myrmica ruginodis* and *Tetramorium* cf. *caespitum*, were common for both assemblages. The fundamental difference between the ant assemblage of the control site and two former assemblages was the local high abundance and proportion (almost 69%) of *Formica fusca* – a submissive species, and at the same time a common slave species of *F. sanguinea*. *Formica fusca* was totally absent from the area inhabited by *F. sanguinea* and almost absent (only one nest found) within the adjacent territory of *L. fuliginosus* (Tables 1-2).

Altogether 129 nests of 10 subordinate species were found at site P (Table 1). Amongst these five subordinate ant species occurred within the territory of *L. fuliginosus* at colony P, and ten species on the control site (Table 1). The 50% drop in the number of subordinate ant species within the *L. fuliginosus* territory in relation to the control area was accompanied by as much as 11.5-fold decrease in the total (compiled) nest density (3.9/100 m² within *L. fuliginosus* territory vs 44.8/100 m² in the control area). The latter was mainly caused by complete absence of the most abundant species on the control site: *Temnothorax crassispinus*, *Leptothorax acervorum* and *Tetramorium* cf. *caespitum*. Thus, *Myrmica ruginodis* became the numerically dominating species among subordinated ants within the *L. fuliginosus* territory. Even so its nest density was still 2.2 times lower there, than outside the territory (Table 2).

Comparison of communities

The number of ant nests was significantly higher in the area controlled by *Formica sanguinea* than in the territory of *L. fuliginosus* according to the GLMM analysis (z = 2.89, p = 0.011). On the other hand, there were no significant differences in this respect either between the *F. sanguinea* area and control areas (z = 1.01, p = 0.31), or control areas and *L. fuliginosus* territories (z = 2.09, p = 0.07), although in this latter case the difference was close to significant.

Species diversity of ant assemblages was generally much higher outside, than within *L. fuliginosus* territory based on the Shannon-Wiener general entropy values. In the case of site F the highest diversity was recorded for the assemblage of the *Formica sanguinea* area (1.71) followed by *L. fu- liginosus* territory (1.33), whereas it was the lowest at the control area (0.83). As for site P, where quadrats of three different sizes were used, values of the index were also higher outside than within the territory of *L. fuliginosus* in each case: 1.69 vs 0 for 1 m², 1.19 vs 0.45 for 10 m², and 1.29 vs 1.06 for 100 m² quadrats, respectively.

Based on the RDA results at site F the ant assemblage of the *Formica sanguinea* area was characterized by the majority of species, mostly by

Table 1. Ant species (not including *L. fuliginosus* and *F. sanguinea*) and numbers of their nests recorded by searching quadrats at the study sites. In the case of site P asterisks mark the values that were used for the calculation of nest densities of particular ant species; n/a – not applicable.

Site	Species	Within *L. fuliginosus* territory			Outside *L. fuliginosus* territory					
					F. sanguinea area			Control area		
		1 m²	10 m²	100 m²	1 m²	10 m²	100 m²	1 m²	10 m²	100 m²
F	*Formica fusca*	n/a	1	n/a	n/a	–	n/a	n/a	9	n/a
	Lasius flavus		7			2			–	
	Lasius niger		–			7			–	
	Leptothorax acervorum		–			1			–	
	Leptothorax muscorum		1			–			–	
	Myrmica lobicornis		1			2			2	
	Myrmica lonae		–			1			–	
	Myrmica ruginodis		4			6			2	
	Tetramorium cf. *caespitum*		3			5			–	
	Total		17			24			13	
P	*Camponotus herculeanus*	–	–	–	n/a			–	–	1*
	Formica fusca	–	1	3*				–	2	7*
	Lasius flavus	–	–	1*				1	2*	5
	Lasius platythorax	–	–	–				1	2*	6
	Lasius umbratus	–	–	1*				–	–	1*
	Leptothorax acervorum	–	–	–				1*	–	–
	Myrmica rubra	–	–	2*				1	1*	7
	Myrmica ruginodis	3	5*	14				2	11*	42
	Temnothorax crassispinus	–	–	–				5*	–	–
	Tetramorium cf. *caespitum*	–	–	–				1*	–	–
	Total	3	6	21				12	18	69

Table 2. Mean ant nest densities (D – number of nests per 100 m²), and SD in brackets, and relative abundance of nests (%) of different ant species, other than *L. fuliginosus* and *F. sanguinea*, at the study sites (for site F – based on data from ten-square metre quadrats, for site P – based on compiled data from one-, ten- and hundred-square metre quadrats; see Data management).

Site	Species	*L. fuliginosus* territory		*F. sanguinea* area		Control area	
		D	%	D	%	D	%
F	*Formica fusca*	0.5 (0.2)	5.9	–	–	6.4 (1.0)	69.2
	Lasius flavus	3.5 (0.7)	41.2	1.0 (0.3)	8.3	–	–
	Lasius niger	–	–	3.5 (0.5)	29.2	–	–
	Leptothorax acervorum	–	–	0.5 (0.2)	4.2	–	
	Leptothorax muscorum	0.5 (0.2)	5.9	–	–	–	–
	Myrmica lobicornis	0.5 (0.2)	5.9	1.0 (0.3)	8.3	1.4 (0.3)	15.2
	Myrmica lonae	–	–	0.5 (0.2)	4.2	–	–
	Myrmica ruginodis	2.0 (0.4)	23.5	3.0 (0.6)	25	1.4 (0.3)	15.2
	Tetramorium cf. *caespitum*	1.5 (0.4)	17.6	2.5 (0.4)	20.8	–	–
	Total	8.5		12.0		9.3	
P	*Camponotus herculeanus*	–	–	n/a		0.2 (0.4)	0.4
	Formica fusca	0.6 (0.5)	15.4			1.4 (1.1)	3.1
	Lasius flavus	0.2 (0.4)	5.1			1.0 (0.3)	2.2
	Lasius platythorax	–	–			1.0 (1.3)	2.2
	Lasius umbratus	0.2 (0.4)	5.1			0.2 (0.4)	0.4
	Leptothorax acervorum	–	–			5.0 (0.2)	11.3
	Myrmica rubra	0.4 (0.5)	10.2			0.5 (0.2)	1.1
	Myrmica ruginodis	2.5 (0.5)	64.2			5.5 (0.6)	12.3
	Temnothorax crassispinus	–	–			25.0 (0.5)	55.8
	Tetramorium cf. *caespitum*	–	–			5.0 (0.2)	11.2
	Total	≈ 3.9				≈ 44.8	

Lasius niger, *Leptothorax acervorum*, *Myrmica lonae* and partially *Tetramorium* cf. *caespitum*, while only *Lasius flavus* was characteristic for the territory of *L. fuliginosus* (Fig. 3). Species like *Formica fusca* and *Myrmica lobicornis* seemed to be closer related to the control area. In the case of site P the picture

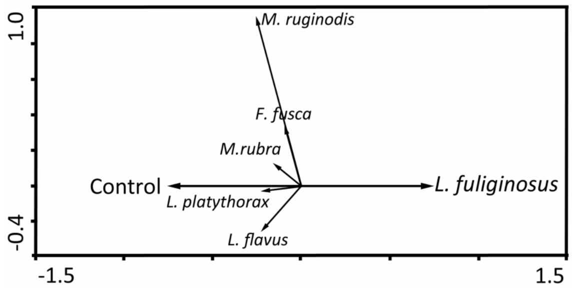

Figure 3. Redundancy analysis (RDA) graph for ant assemblages at site P.

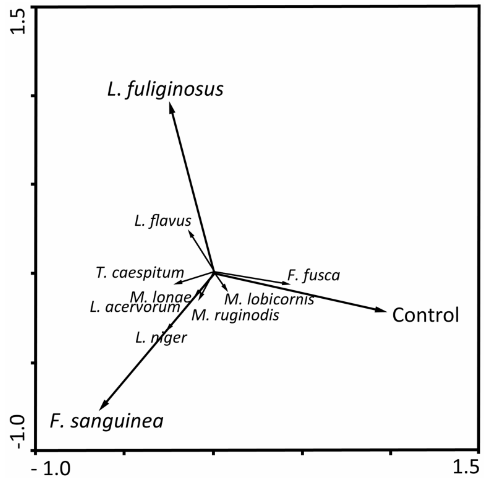

Figure 4. Redundancy analysis (RDA) graph for ant assemblages at site F.

was basically the same, but involving slightly different set of species. Most ant species were related – however with different strength – to the control area; the least related species to the *L. fuliginosus* territory were *Lasius platythorax* (sister species of *L. niger*) and *Myrmica rubra* (Fig. 4).

Generally the nest number of subordinate species significantly depended on the RDA axes representing the sampling area (*L. fuliginosus* territory, *F. sanguinea* area and control area) at site F (Monte Carlo test, trace = 0.112, F = 3.211, p = 0.002). On the other hand such relationship could not be revealed for site P (trace = 0.054, F = 2.185, p = 0.106).

Discussion

Territorial species are the top dominant of ant assemblages within areas controlled by their colonies and thus they exert noticeable negative influence on co-occurring subordinate species. Although in this topic many studies focus on wood ants (e.g. Savolainen & Vepsäläinen 1988, 1989, Pisarski & Vepsäläinen 1989, Savolainen et al. 1989, Punttila et al. 1996, Vepsäläinen et al. 2000), similar role in assemblages plays *L. fuliginosus* (e.g. Czechowski et al. 2013). The present study, based on two *L. fuliginosus* colonies (one in Finland, the other in Poland), combined with already published findings based on one more Finnish colony (Czechowski et al. 2013, Markó et al. 2013) showed that the adverse effect of this top competitor on subordinates manifests itself in decreasing abundances of the latter, up to complete exclusion of some species. This can lead to deep restructuring of the whole assemblages, including decrease in the total nest density, impoverishment of the species composition and a reshuffle in the dominance structure. Subordinate ant species of the two lower tiers of the competition hierarchy, i.e. both encounters (e.g. *Lasius niger*, *L. platythorax*, *Tetramorium* cf. *caespitum*) and submissives (e.g. *Myrmica* spp., *Leptothorax acervorum*, *Temnothorax crassispinus*, *Formica fusca*) may suffer serious losses.

Two combined (hardly separable) main mechanisms of persecution of subordinates may act in *L. fuliginosus*: (a) competition (especially of the interference or contest type) and (b) predation. By analogy to wood ants it can be assumed, that the first mechanism is directed mainly against encounter species, which, in the nature of things (as defending food resources), are most competitive toward territorials. Such species, especially *Lasius niger* or *L. platythorax*, are known to be often close to non-existent within wood ant territories (Savolainen & Vepsäläinen 1989, Savolainen et al. 1989, Väänänen et al. 2010). Wood ants, restricting food availability, also inhibit development of colonies and decrease production of sexuals of the submissive species (Savolainen 1990). Pressure of *L. fuliginosus* on *Formica fusca*, judging from some observations, may be even stronger than that of wood ants (see below).

The other mechanism that operates together with interspecific competition in structuring local ant assemblages is predation. It should be noted that in ants it is difficult to separate predation (in the meaning of myrmecophagy) and competition, and as such predation is very often inextricably linked to competitive conflicts for food, nest sites and territory (Vepsäläinen 1980). On the other hand, ants often prey upon other ants (both inter- and intraspecifically) when ordinary food resources are insufficient (see Carrol & Janzen 1973). *Lasius fuliginosus* belongs to species to which organized predatory attacks on other ant colonies come so easy, that it can be regarded as a facultative myrmecophage (Czechowski 2002). There are observations of its successful (leading to mass robbery of brood or callows) predatory attacks on colonies of *Myrmica* spp. (e.g. *M. rubra*, *M. schencki*), *Temnothorax tuberum*, a colony of the slave-maker *Harpagoxenus sublaevis* mixed with its slaves *Leptothorax acervorum*, and even an incipient colony of *Formica sanguinea* mixed with its slaves *F. fusca* (Wasmann 1899, Czechowski 2002, Markó et al. 2013). Additionally, hostile *L. fuliginosus* expeditions, although unsuccessful (the attacked ants barricaded themselves with sand inside the nests), were seen also on nests of *Lasius niger* and *L. psammophilus* (Czechowski 2002). It seems that *L. fuliginosus* owes its relatively easy successes to dendrolasin, a peculiar deterring and irritant chemical weapon (Pavan 1959; see also Czechowski 2000a).

Myrmecophagy of *L. fuliginosus* is the most probable mechanism, which can explain complete lack of the submissives *Temnothorax crassispinus* and *Leptothorax acervorum*, and maybe even that of the encounter species *Tetramorium* cf. *caespitum*, within the territory of the colony studied in Poland – whereas these species abundantly occurred just near the *L. fuliginosus* territory. This phenomenon might be also responsible for the noticeably reduced nest density of *Myrmica* species within both studied *L. fuliginosus* territories (see Table 2).

Combination of competition with predation in *L. fuliginosus* causes, that its colonies equally well control colonies of the encounter species (e.g. *Lasius niger*, *L. psammophilus*), which are directly most competitive to them, as colonies of submissives (like species of the genera *Myrmica*, *Leptothorax*, *Temnothorax*). Otherwise, wood ants first of all tend to exclude encounter species (Savolainen & Vepsäläinen 1988, 1989, Savolainen et al. 1989). They seem to be much more 'tolerant' to submissives, such as *Myrmica* and *Leptothorax* species, due to their different food requirements, foraging strategies and certain behavioural features, which allow some spatial separation (Savolainen & Vepsäläinen 1989, Kiss & Fetykó 2008). It is known that *Leptothorax* (and, by analogy, probably also *Temnothorax*) species may even associate with wood ants due to their diminutive size and furtive behaviour (Vepsäläinen & Pisarski 1982, Seifert 2007), supposedly benefiting by collecting small left-over food particles from the larger partner. Moreover, they may get protection from wood ants against ant species which are closer to their own size (Savolainen & Vepsäläinen 1989), including protection against raids of the slave-maker *Harpagoxenus sublaevis* (Punttila et al. 1996). In the case of *L. fuliginosus*, its own predatory inclination towards other ants rather excludes a possibility of such protection (see Markó et al. 2013).

Territorial ant species, by defending their own territories, also interfere with raids of *Formica sanguinea*, thus colonies of potential slave species (i.e. those of the subgenus *Serviformica*) gain indirect protection against being raided. Such interferences were observed both in wood ants (*Formica rufa*) and *L. fuliginosus* (just in the currently discussed colony F) and they manifested in holding back or forcing a raiding *F. sanguinea* column to by-pass the foreign territory (Czechowski 1999, 2000a). Interestingly, the attitude of *Serviformica* ants towards *L. fuliginosus* depends on the competitive status of a given *Serviformica* species. When nests of *Formica cinerea* and *F. fusca* were raided close to the *L. fuliginosus* territory and workers of both species fled side by side straight ahead, the *F. cinerea* individuals never crossed the boundary, whereas *F. fusca* got freely far inside the territory (Czechowski 1999). *Formica cinerea*, although subordinated to typically territorial ants, is a quite aggressive species, even with some territorial tendencies (see Markó & Czechowski 2004, 2012, Czechowski & Markó 2005). On the other hand, *F. fusca* is a typically submissive non-aggressive species (e.g. Savolainen 1990, 1991).

At the population level, shelter given *Formica fusca* by territorial ant species on areas threatened with raiding activity of *Formica sanguinea* should be detectable as higher abundances of *F. fusca* within than outside their territories, as was found in the case of wood ants (Czechowski & Vepsäläinen 2001, Czechowski & Markó 2006, Väänänen et al. 2010). However, such protective effect towards *F. fusca* from the side of the studied *L. fuliginosus* colony in Finland was not revealed – even so that very colony F was earlier seen to stop raiding *F. sanguinea* columns or to force a column to go around its territory, and to let *F. fusca* escapees into the territory (Czechowski 1999, 2000a). The single *F. fusca* nest found within the *L. fuliginosus* territory vs zero outside the territory is of no importance – particularly when taking into consideration that *F. fusca* nest density was as high as 6.4 nests/100 m^2 in the control area out of the range of both *L. fuliginosus* and *F. sanguinea* (see Table 2). These data imply that, at least in the case of this particular colony of *L. fuliginosus*, the possible protective effect of *L. fuliginosus* on *F. fusca* against *F. sanguinea* raids does not compensate its direct negative effect on this submissive species. This, in turn, may suggest that the negative competitive effect of *L. fuliginosus* on the submissive *F. fusca* can be much stronger than that of wood ants. This seems highly probable, especially in the light of the recent studies on the two territorials, *L. fuliginosus* and *Formica polyctena*, and their effect on subordinate species within their adjacent territories (Czechowski et al. 2013, Markó et al. 2013). In the context of the present study, the most spectacular result of the latter paper was that although *F. fusca* was frequently foraging on the territory of *L. fuliginosus*, it was rather rarely nesting there (Markó et al. 2013). In wood ant territories situation is quite different: there *F. fusca* colonies – although with evidently lower fitness – can nest even close to the wood ant mounds (Savolainen 1990, 1991; see also Czechowski & Vepsäläinen 1999, Czechowski 2004).

All things considered, *L. fuliginosus* seems to shape ant assemblages on its territories in a much more severe way than either *Formica sanguinea* or wood ant species generally. Nest count and density data and diversity values all point in one directions: *L. fuliginosus* impoverishes ant assemblages by combining competitive pressure with drastic predation on co-occurring ant species. The question is still open though: are there any specific adaptations that help submissive ant species to maintain their colonies on territories of this top dominant? Could shifts in spatial and temporal activity patterns or behavioural modifications help the survival of submissives as suggested by the recent observation of Vepsäläinen & Czechowski (2014) in the case of *Myrmica rugulosa*? Future studies may focus on such possible adaptations.

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