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Intra- and interspecific relationships in *Formica exsecta* Nyl. (Hymenoptera: Formicidae) supercolonies

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1 Polydomy in ants

Although worldwide many ant species are known to form large polydomous systems comprised of many interrelated nests (e.g. *Formica yessensis* Wheeler, 1913 and *Lasius sakagamii* Yamauchi and Hayashida), in Europe only a handful of ant species develop polydomous systems (Seifert 2010). Among European well-known native polydomous ant species are *Liometopum microcephalum* (e.g. Petráková and Schlaghamerský 2011), *Lasius fuliginosus* (e.g. Czechowski et al. 2013) and many species from the genus *Formica* (e.g. Cherix 1980; Rosengren and Pamilo 1983; Rosengren 1986; Savolainen and Vepsäläinen 1989; Sundström 1993; Markó et al. 2012). Ecologically dominant native ants are often polydomous, and nest relocation and the maintenance of multiple nests both play a role in their competitive success (Debout et al. 2007; Helanterä et al. 2009; Buczkowski 2012; Boulay et al. 2014; Robinson 2014).

Polydomy implies the existence of a plethora of specific features in ant species (Debout et al. 2007; Helanterä et al. 2009). In most of these species, polydomy and polygyny are correlated because polygynous colonies reproduce by budding (Alloway et al. 1982; Rosengren and Pamilo 1983; Helanterä et al. 2009). Polydomy often coincides with the loss or shorter range of nuptial flight in gynes, and with queens and males mating inside or in the close vicinity of the nest, while queens would not disperse far after mating (Chapuisat and Keller 1999). Colonies of such species usually reproduce through budding, where the daughter nests are formed by a fraction of workers and queens originating from the mother nest (Higashi 1979; Ross and Keller 1995). The newly formed daughter nests usually remain in social contact with the mother nest (Rosengren and Pamilo 1983; Pamilo 1991), and exchange workers, brood and food for several years (Liautard and Keller 2001, Gyllenstrand and Seppä 2003).

Polydomy can empirically be identified in the field based on the overdensity of same-species neighbors, the existence of shorter internest distances with very high mound densities, associated with huge number of workers, which often cover several hectares (Pisarski 1982; Savolainen and Vepsäläinen 1988; Hölldobler and Wilson 1990). Polydomous colonies range from the simplest structure, made up of two or few connected nests, to complexes of many thousands of nests (Markó et al. 2012; Giraud et al. 2002).

The social connections between polydomous colonies can be broadly categorized into three types: (a) resource sharing (e.g. food, nest material) (e.g. Erős et al. 2009, Csata et al. 2012), (b) exchange of colony members (e.g. queens, broods, workers, particular task groups) (Pisarski 1982, Debout et al. 2007, Kümmerli and Keller 2007), and (c) information sharing (e.g. recruitment of workers to food) (Robinson 2014).

Polydomy can also be perceived as cooperation between separate parts of a colony evolutionary selected for to avoid conflict across nests, which would hinder the monopolization of resources (Debout et al. 2007; Erős et al. 2009). The lack of aggression (Astruc et al. 2001; Holzer et al. 2006) is evolutionary advantageous since aggression is costly, involving direct and indirect losses, while high accuracy non-nestmate discrimination system is needed in order to avoid recognition errors (Reeve 1989). The absence of intraspecific aggression within supercolonies leads to high population density, reduces costs associated with maintaining territoriality, and ultimately leads to increased colony size, which is key to the ecological dominance in ants (Holway et al. 1998; Holway 1999; Steiner et al. 2007).

Polydomy has numerous ecological advantages, in terms of colonization ability (Holway 1999; Giraud et al. 2002), resource exploitation (Hölldobler and Lumsden 1980; Holway and Case 2001; Elis et al. 2014) and interspecific competition (Holway 1999; Markó et al. 2013; Ślipiński et al. 2014). Consequently, supercolonial ants indeed are among the ecologically most successful organisms (Tsutsui et al. 2000; Debout et al. 2007; Helanterä et al. 2009).

Socially connected nests can provide quick and low-risk spreading into a new area (Holway and Case 2000). The distribution of individuals and broods across nests may reduce the risk of colony extinction (Droual 1984; Cerdá and Retana 1998), which makes the colony less reliant on the survival of any particular nest, thus increases the resiliency of the system. Through this switch to dispersed central-place foraging behaviour from an entirely central-place foraging strategy, the supercolonial system becomes more flexible (McIver 1991; Holway and Case 2000; Pfeiffer and Linsenmair 1998; Buczkowski and Bennett 2006). Thus, such ant species are thought to achieve energetic savings by decentralization (Hölldobler and Lumsden 1980), especially by reducing the overlap in the individual foraging paths (Traniello and Levings 1986; Davidson 1997), thereby increasing their foraging efficiency, competitive ability and effectiveness in defending resources form competitors (Cherix and Bourne 1980; Rosengren, 1986; Cao 2013). A polydomous colony can forage over a greater area on more diverse food resources, and thereby it stabilizes the colony's food supply (Holway and Case 2000; Cerdá et al. 2002). In particular, red wood ants of the subgenus *Formica* s. str. construct elaborate nests, and increase their food supply by tending aphids thus developing large supercolonies (Pisarski 1982). Such conditions may lead to the monopolisation of patches of habitat (Chapuisat and Keller 1999; Pfeiffer and Linsenmair 2001), as in the case of red wood ants, which dominate entire forests.

The main aim of our study was to investigate the specific features of intra- and interspecific relationships within polydomial *Formica* ant nest systems, mostly in *F. exsecta*.

2 Study species

Our study species *Formica* (*Coptoformica*) *exsecta* Nylander, 1846, the narrow-headed ant, is a relatively common mound-building, pan-Palaearctic ant species. Both monogynous and polygynous colonies are frequent in *F. exsecta*; the latter can develop into large polydomous systems (Werner et al. 1979; Chudzicka 1982; Pisarski 1982; Skibińska 1982; Czechowski 1990; Seifert 2000; Bliss et al. 2006; Goropashnaya et al. 2007; Kümmerli and Keller 2007; Martin et al. 2009). One nest can contain from several hundred to several hundred thousand individuals, and in polygynous nests, the number of queens can reach several dozen (Pisarski 1982; Sorvari 2009). In the polygynous form, colonies may extend through nest splitting. Large aphid colonies and a high stability of the aphid source are usually needed for the development of such polydomous systems (Pisarski 1982). *Formica exsecta* supercolonies can effectively displace other ant species, as well as other arthropods, from their territory (Pisarski 1982).

3 Study site

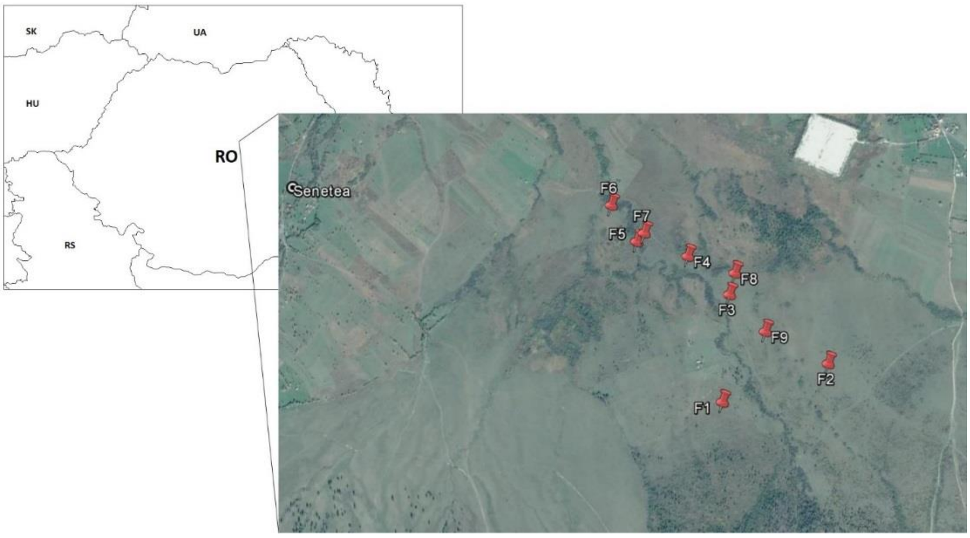

Fig. 1. *Map of the studied Formica exsecta population (46°36'N, 25°36'E, Harghita County) with the polydomous systems (© Google Earth).*

Our investigations were carried out mainly in the southern part of the Giurgeului depression, in the eastern Carpathians, near the village of Voslobeni (Harghita County, Romania, 46°36'N, 25°36'E, 780 m a.s.l., Fig. 1). There are at least nine large polydomous systems of *F. exsecta* in the southern part of the depression. The smallest polydomous system comprised 12 nests, while the largest, and comprised more than 3000 nests, stretching over more than 22 ha. Several aspects of polydomy have already been studied in the case of the supercolony selected for the purpose of this study (Goropashnaya et al. 2007, Erős et al. 2009, Martin et al. 2009; Csata et al. 2012; Kiss and Kóbori 2012). The results of these studies are consistent with the general knowledge regarding polydomy. Thus, intranest relatedness of workers is low (r = 0.22 ± 0.06) (Goropashnaya et al. 2007), and the level of aggression is reduced between ants originating from different nests of the polydomous system (Martin et al. 2009; Kiss and Kóbori 2012). The density of ant nests and aphid colonies can reach extreme values in specific parts of this system, and feeding grounds overlap to a great extent (Erős et al. 2009). *Formica exsecta* also builds outstations near aphid colonies, usually at the root of the aphid-housing plants (Csata et al. 2012). At the high density site outstations belonged to more ants nests, which, ultimately, could result in higher intensity of information flow among different nests. In the view of our previous results (BSc- and MSc-thesis) outstations act like localized information exchange centers, which contribute to the integration of nests within a supercolonial system (Erős et al. 2009; Csata et al. 2012). *F. exsecta* has a negative effect on ant communities of the supercolonies (Pisarski 1982; Czechowski et al. 2013; Markó et al. 2013), it influences the presence or the abundance of sub-dominant ant species, and can cause significant changes in their foraging behaviour (Czekes et al. in prep; Maák et al. in prep.).

Table 1. The features of the studied nine supercolonies.

Site code	Area (m^2)	No. of nests	Density (nests/ha)	Mean nest mound diameter
F1	220000	3347	152	55.11 (SD ±57.04)
F2	19300	~400	207	46.46 (SD ±56.01)
F3	1940	37	191	40.51 (SD ±45.58)
F4	660	18	273	37.94 (SD ±26.59)
F5	4900	74	151	30.60 (SD ±24.05)
F6	1670	20	119	48.20 (SD ±33.76)
F7	1130	18	159	12.69 (SD ±6.78)
F8	3600	67	186	29.77 (SD ±26.80)
F9	840	15	179	47.73 (SD ±34.44)

The main subjects of the present study, the *F. exsecta* supercolonies are located in a fen meadow with *Molinia caerulea*, *Deschampsia caespitosa*, *Festuca pratensis*, *Briza media*, *Nardus stricta*, *Succisa pratensis*, *Filipendula ulmaria*, *Stachys offiinalis*, and *Cirsium palustre* as the most abundant or characteristic plant species. The sites are overgrown with scattered small trees and saplings of *Betula pubescens*, *Picea abies*, *Frangula alnus*, and *Salix* spp. The meadows are fairly intensely grazed by cows for most of the year (Fig. 2).

4 Results

4.1 The largest polydomous system of *Formica* ants in Europe

Our primary aim was (1) to reveal how unique the recently discovered *Formica exsecta* population is in Europe, which comprises nine polydomous colonies (see Fig. 1). We hypothesized that differences in ant nest density within a supercolony could result in differences regarding the number of connections an ant nest has with other nests e.g. through shared aphid colony tending.

Based on our results, the supercolony presented here is by far the largest known European polydomous system not just for this species, but most probably for all mound building territorial *Formica* species. The entire population is remarkably large; it could well be one of the largest *F. exsecta* populations in Europe.

The presence of aphid colonies together with other rich food sources may shape ant communities by allowing aphid-tending ants to become numerically (and, in the case of certain species, also behaviorally) dominant, reducing the abundance and success of other ant species (Banschbach and Herbers 1996). Under optimal conditions, colonies of certain aphid-tending ants can develop into large polydomous systems (Pisarski 1982; Debout et al. 2007). These factors, among others, could have led to the formation of these *F. exsecta* supercolonies (Erős et al. 2009). Although mostly stable, such polydomous systems show certain variations in time and space that can be attributed to some extent to the dynamics of the aphid sources (Bönsel 2007; Vepsäläinen and Savolainen 1994; Czechowski and Vepsäläinen 2009). In this supercolony, very few changes occurred in the number of *F. exsecta* nests compared to a previous study period reported in Erős et al. (2009). The relatively high stability found for the ant nests suggests suitable habitat conditions, with the persistence of available food sources possibly being one of the most important stabilizing factors.

It is reasonable to assume that biases in ant-nest distribution and size within supercolonies can be caused by heterogeneity in the distribution and availability of permanent food sources, e.g., aphid colonies. For example, Werner et al. (1979) showed that *F. exsecta* nests tend to be aggregated around trees within a polydomous system, not just because of the better climatic conditions, but also because of the richer aphid sources. The *Formica exsecta* population presented here seems extremely healthy and stable due to high ant nest density and ant nest number.

4.2 Habitat characteristics of polydomous systems in *Formica exsecta*

Habitat characteristics influence also the composition and stability of ant communities, species abundance and also the development of specific social structures (Boomsma and van Loon 1982; Hölldobler and Wilson 1990; Bönsel 2007). A variety of ecological factors may favor the spatial separation of a colony (Cerdá et al. 2002). Polydomy has often been considered as a response to various environmental constraints, and several hypotheses have been proposed. But how could such large polydomous system develop in a relatively restricted area? Thus, further on we were interested to find out (1) which habitat features could contribute to the formation and stability of such polydomous systems? (2) Can a set of optimal habitat characteristics be identified based on *F. exsecta* nest density and nest size? (3) Is there any specific traditional land use strategy, which helps them survive and develop?

Fig. 2. *Typical habitat of a Formica exsecta supercolony in the study region.*

On the basis of our results *F. exsecta* polydomous systems develop in grazed, open areas with low shrub-coverage and reduced shrub height (Fig. 3). The traditional low intensity grazing controls the height and cover of shrubs, thus prevents the development of forests, which are un-habitable for *F. exsecta*. Thus, to some extent, grazing by cows could be beneficial for *F. exsecta* supercolonies, as it keeps trees and shrubs below a certain height. However, too intense grazing can represent a major threat for this species (Werner et al. 1979; Erős et al. 2009). Trampling by cows can reduce vegetation cover and prevent nests from budding by destroying incipient nests. The features (no. of nests, nest density, nest size) of the studied polydomous systems are unique in Europe, which shows that the habitat conditions are optimal for *F. exsecta*. The results of our study could further on be used for the elaboration of an appropriate conservation plan of the studied *F. exsecta* polydomous systems. The relatively high stability of the ant nests in these supercolonies suggests suitable habitat conditions, with the persistence of available food sources possibly being one of the most important stabilizing factors (Erős et al. 2009).

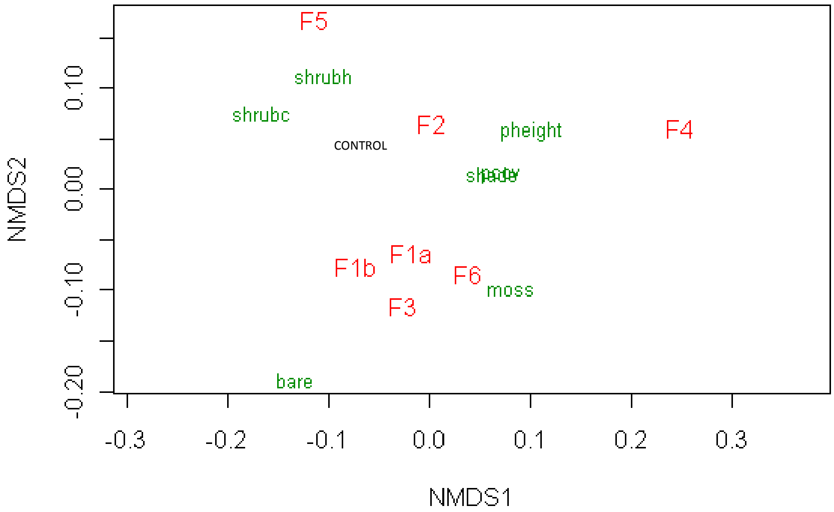

Fig. 3. *NMDS ordination of study sites based on vegetation parameters (Bray-Curtis similarity, stress = 2.52). Abbreviations: shade – shading, pcov – plant cover, pheight – plant height (excl. shrubs), moss – moss cover, bare – bare ground cover, shrubh – shrub height, shrubc – shrub cover.*

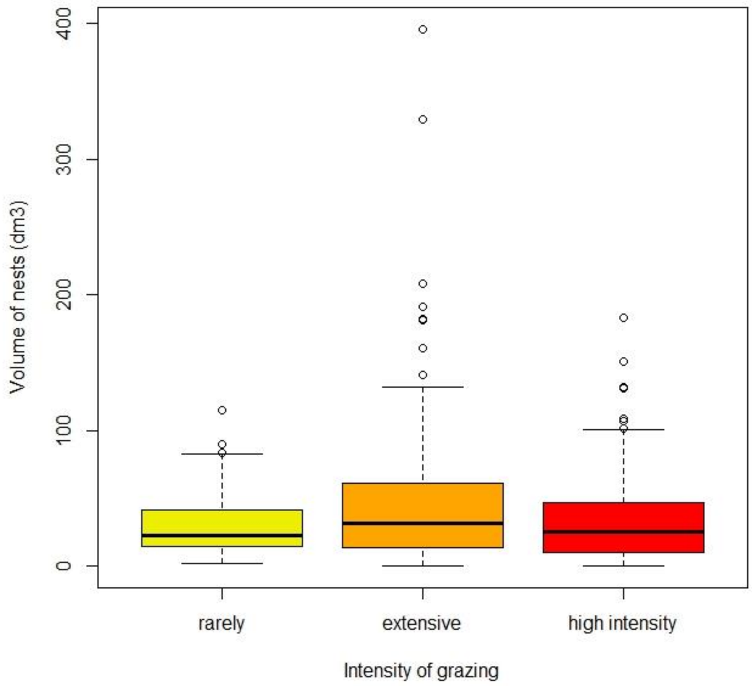

Fig. 4. *The size of ant nests in different intensity grazed sites.*

Nevertheless, the recent changes in Romanian agriculture, which have caused a drastic decrease in cow numbers and consequently abandonment of traditional extensive grazing and haymaking techniques, additionally the illegal burning. These changes may affect the size of *F. exsecta* nests (Fig. 4) and their density (Fig. 5). These changes may endanger the survival of this unique population in the long run, as proven in other related species (Bönsel 2007). Thus, only the implementation of an appropriate management plan could help the survival of this unique social system.

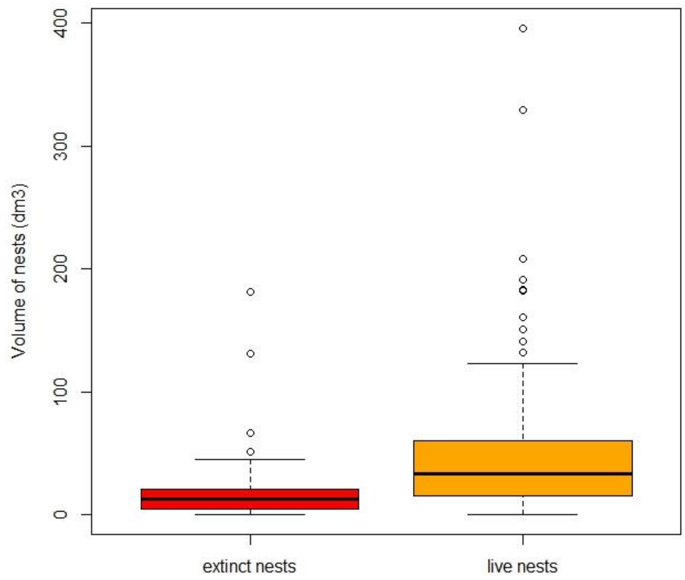

Fig. 5. *The mound volume of dead and survived nests after illegal arsen.*

4.3 The key to cooperation: nestmate and non-nestmate discrimination within a supercolonial system

The lack of aggression and recognition of kins on the basis of a simple cues among non-nestmate workers within polydomous systems is well-known. The colony odour plays a key role in ensuring the social cohesion and, therefore, it is at the basis of altruistic behaviour within a society (Beye et al. 1997; Mateo 2004), whether constituted by a small family group or by millions of individuals. In ants, the cues responsible for colony-mate recognition are specific bouquet of cuticular hydrocarbons (CHC-profile), which has an inherited and an acquired component (Lahav et al. 1999; Wagner et al. 2000; Lenoir et al. 1999). Polydomy, however, poses an intriguing problem, since workers must recognize not only nestmates residing in the same nest, but also those living in other nests (Beye et al. 1997). The small differences occurring between workers coming from different parts of a supercolony could not be mirrored by other behavioral acts as e.g. antennation, which is known to be the first step to discrimination (Boulay et al. 2000; Holzer et al. 2006). (1) Does the length of intraspecific interactions show some variations within an exceptionally large supercolonial system, and, more importantly (2) could the duration of antennations reflect, as suggested above, the process of updating recognition cues in case of encounters where individuals are coming from distant nests? (3)

The level of aggression was very low among non-nestmate *F. exsecta*, almost no aggression was registered against conspecific individuals. This leads us to the conclusion that, as stated by Kiss and Kóbori (2011), the *F. exsecta* nest-complexes, which are more than 500 m away from each other, are forming a meta-nest-complex.

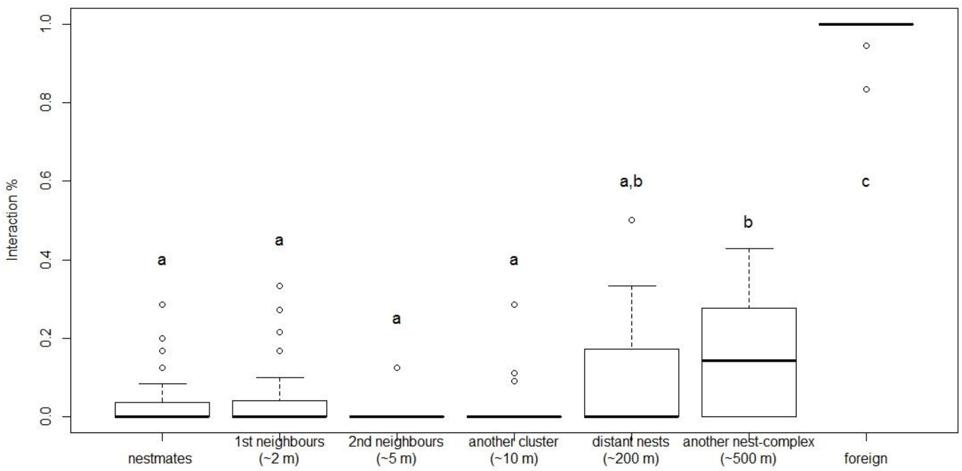

Fig.6. *Aggression indices based on the frequency of aggressive interactions (different letters indicate significant differences).*

There was, though, a slight but not significant increase in the aggressiveness with increasing distance (Fig. 6), which might indicate that there is a slight separation between these nest-complexes, yet this is not enough for rejection. The lack of intraspecific aggression is even more emphasized when the registered aggression levels are compared to the aggression recorded in the case of interspecific encounters, where, indeed, aggression peaked.

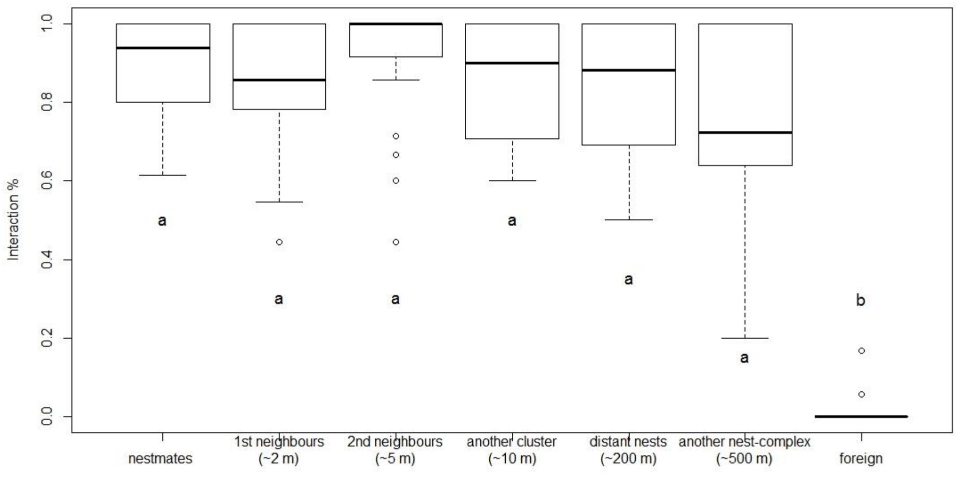

Fig. 7. *Antennation indices based on the frequency of antennations (different letters indicate significant differences).*

The data on antennation behaviour showed also no significant increase in the duration of bouts between nestmates and non-nestmates, between nests of different nest-complexes (Fig. 7). The lack of differences in the peaceful mutual investigation by antennation between ants from different nests might be caused by small differences in colony odor. This study supports that our study system can indeed function as a supercolony, since ants there is mutual acceptance among ants coming from various parts of the same system, but they are even tolerant to workers from different system of the same population.

4.4 Potential antimicrobial properties of *Formica exsecta* nest mound's plant material

The social system of ants is an attractive target for many parasites due to the high abundance of potential host organisms and the spatial stability of nests (Buschinger 2009; Boomsma et al. 2014). A polydomous system is made up of high number of related ant nests, which are connected through permanent worker and information exchange that (Kümmerli and Keller 2007) could promote the dispersal of parasites (Schmid-Hempel 1995). Parasites can dramatically reduce host fitness, therefore hosts are expected to evolve protective mechanisms and behavioral adaptations that reduce the risk of infection or minimize parasite-induced fitness loss. In addition to immune defense mechanisms, the use of plant metabolites is also known to be efficient in many cases against pathogens (Clark 1991; Huffman 2003). It is known that wood ants species nest mound building is associated with frequent needle turnover and they collect and incorporate antimicrobial plant resin from conifer trees into their nests, which prevents and reduces microbial growth, and can the increase the survival chances of parasitized individuals (Christe et al. 2003; Chapuisat et al. 2007; Castella et al. 2008; Simone et al. 2009; Simone-Finstrom and Spivak 2010; Brütsch and Chapuisat 2014). We wished to examine whether the nest material of *F. exsecta* mounds, which contains plant remnants, has some general antimicrobial properties, such as it is known in several bird and mammal species. Our study show a clear negative results. The *F. exsecta* nest mound's plant material does not have any negative antimicrobial effect on microorganisms from the nests or from the soil (Fig. 8). On the other hand, the nest material is heterogeneous, which might explain the large variance in the data and the lack of clear trends.

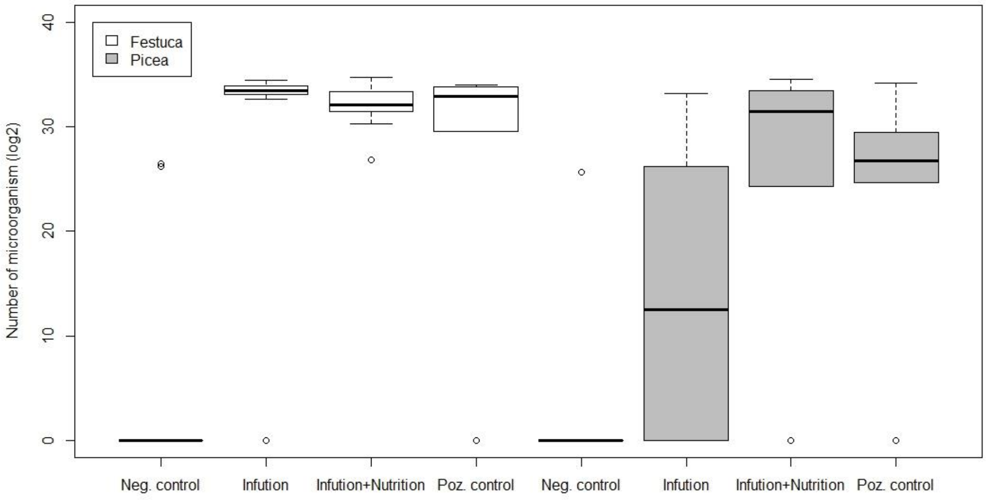

Fig. 8. *The colony number of microorganisms among different treatments with Festuca grass blades and with Picea needles in the autumn samples.*

4.5 Simple defense mechanisms that keep *Pandora's* box closed in an ant nest system parasitized by a highly pathogenic fungus

The lethal endoparasitic fungus *Pandora myrmecophaga* is known from the studied *Formica exsecta* polydomial system (Csata et al. 2012). The fungus manipulates the host in order to ensure its efficient distribution within the supercolony (Roy et al. 2006. Boer 2008). Based on this most efficient transmission mechanism considerable prevalence of the fungus would be expected in a parasitized social system. A hypothesis of a simple social behavioral defense strategy was anecdotally formulated by Marikovsky (1962) based on his field observations and we tested this hypothesis regarding the existence of simple defense mechanism: workers would dispose of every corpse, as potential source of infection, appearing on grass-blades, thus lowering the chances of spore dispersal.

After discovering corpses ants removed them quickly (Fig. 9), and larger nests, which were more active, reacted generally more promptly. The result of this efficient reaction is the prevention of the development of the conidia, which needs at least 2-4 days in natural conditions (Marikovsky 1962, Boer 2008, pers. obs.), but in favourable conditions, with elevated temperature and moisture the spores could develop after one day (pers. obs.). The generality of this prophylactic strategy is very important, since usually specific defense mechanisms are costly.

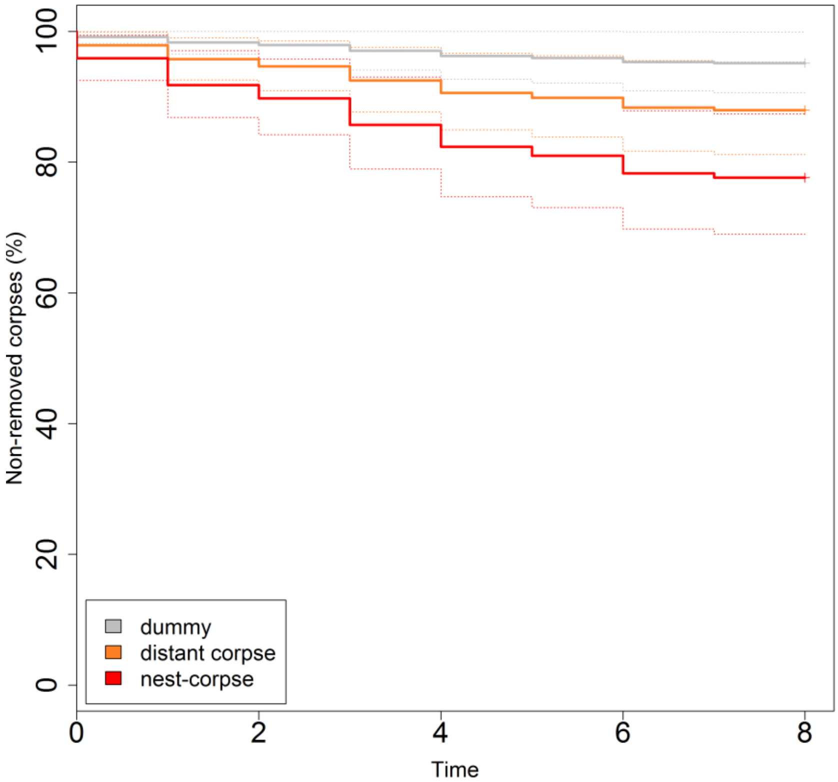

Fig. 9. *Estimated functions for Cox regression of time to corpse removal based on the type of corpses. Broken lines represent a point-wise 95-percent confidence interval around the corresponding functions.*

4.6 Pollen as alternative food source for subdominant ant species in suboptimal circumstances on the territories of polydomous *F. exsecta* and *F. polyctena*

Ants, being so ubiquitous, have the potential to influence plants both beneficially and antagonistically. Thus ants contribute decisively to the dispersal of a wide array of plant species, however, they could also have serious negative impact on plants, especially with regards to the process of on pollination (Beattie et al. 1986; Ashman and King 2005). In order to hinder this impact, many plant species have evolved traits that repel ants (Willmer and Stone 1997; Ghazoul 2001; Raine et al. 2002; Nicklen and Wagner 2006; Wagner and Kay 2002; Ballantyne and Willmer 2012), therefore, regardless of the fact that ants are omnivorous, pollen seems to be very rare in their diet (Czechowski et al. 2011; Cembrowski et al. 2015). We hypothesized that food shortage caused by extreme competitive pressure of polydomous territorial ant species may drive subdominant species to use resources that are not commonly utilized, as pollen. Two supercolonial systems, one of *Formica exsecta* and one of *F. polyctena* offered suitable field conditions to test this hypothesis.

We examined the effect of polydomial *F. exsecta* and *F. polyctena*, which are at the top of the hierarchical competitive system (Cherix 1980; Pisarski 1982; Erős et al. 2009), on foraging strategies of subdominant species, specifically on their pollen utilization, as suboptimal food source. Our main result is that *Myrmaica* species consume pollen and even recruit to it more often and in higher number pollen in patches where the territorial dominates generally the food sources (Fig. 10-11). It has been several times documented in many different species that submissives adapt to the presence of dominants by changing their foraging strategies, e.g. selecting for less rewarding food sources (Savolainen and Vepsäläinen 1988; 1989; Savolainen 1991; Vepsäläinen and Pisarski 1982; Markó and Czechowski 2012; Czechowski et al. 2013; Markó et al. 2013). Such possible alternative source is pollen, which has a high nutritional value (Roulston and Cane 2000), but ants often avoid it possibly because of repellents produced by plants (Junker et al. 2007; Junker and Blüthgen 2008; Willmer et al. 2009). Our results show that indeed submissive species, as e.g. *Myrmica* spp. on the territories of both supercolonies, tend to consume pollen, which is usually avoided or at least markedly less utilized by dominants. On territory of *F. exsecta* other submissive species were also recorded to consume pollen, as *F. cunicularia*, *F. fusca*, and *M. schencki*, while on the territory of *F. polyctena Temnothorax* spp. individuals were seen on pollen in addition to *Myrmica* spp.

We even observed recruitment to pollen by submissive ants: *M. scabrinodis* on *F. exsecta* territory and *Myrmica* spp. on *F. polyctena* territory. When a forager discovers a rewarding food source returns to the nest laying a pheromone trail, and recruits other foragers from the nest, which then follow the discoverer via the previously laid pheromone trail (Beckers et al. 1990). In this way the colony can exploit the food source much quicker, more efficiently (see Beckers et al. 2009, Czaczkes et al. 2015). These observations also confirm that pollen can be attractive in certain conditions.

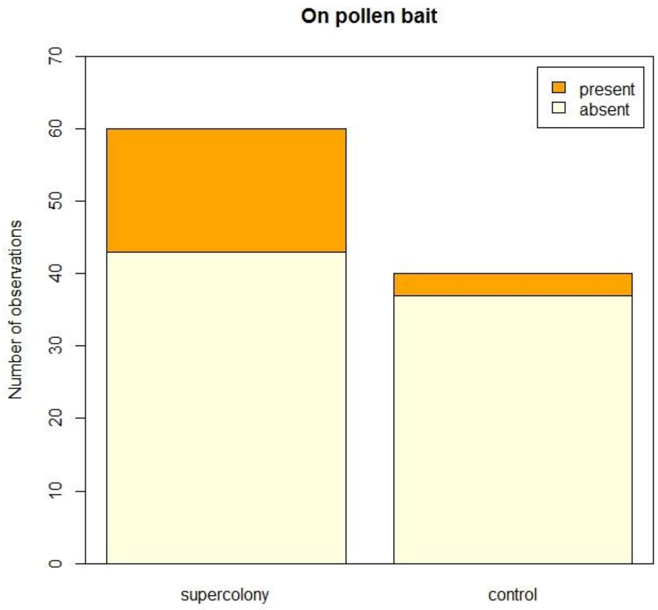

Fig. 10. *Occurrence of ants on pollen baits within the territory of the F. exsecta supercolony and in the control site.*

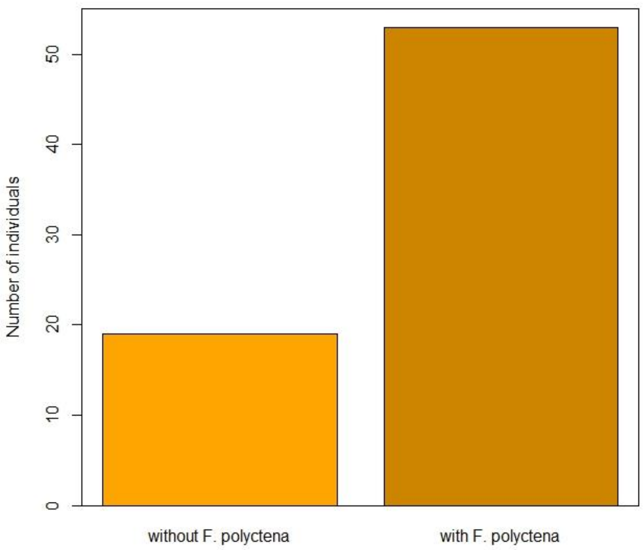

Fig. 11. *Number of Myrmica spp. individuals eating pollen in empty patches and in those dominated by F. polyctena.*

In the frame of our study we demonstrated that the consumption of pollen in ants can be much more frequent than originally thought. In suboptimal circumstances ants could exploit this resource too. In a poorer habitat the submissive species used more the pollen as alternative sources, so pollen constitutes an important food source in such a habitat, where the competition is fiercer. This also underlines the importance of repellent agents produced by plants, since our study demonstrates that in the lack of these agents ants might easily turn to utilize this alternative food source.

4.7 A peculiar natural disturbance factor for supercolonies: brown bears (*Ursus arctos*)

The importance of ants as food source for bears has been recognized for quite a while (Boltunov 1993; Elgmork and Unander 1998; Bojarska et al. 2012). Since a highly dense multi-nest system, as supercolony of *F. exsecta* could constitute a stable, and highly rewarding food source, and the region where it is located is known for its large brown bear population, we can hypothesize that bears would target the supercolony. We proposed to evaluate the potential impact of brown bears on the supercolony by performing a standard census of attacked ant nests.

Out of *F. exsecta* ant nests 916 (56%) mounds were visibly attacked by bears (Fig. 13). The attack proportion seems to be high, though, when comparing it solely to available data on *F. exsecta* (56% vs. 0-2% after Atanassov 1983 in Swenson et al. 1999).

Consequently, our large *F. exsecta* supercolony constitutes an important food source for brown bears in the area. It is not clear though, whether bear attacks could actually be fatal to the *F. exsecta* supercolony on the long run. Regular bear visits of the meadow may, in a strange way, even benefit the supercolony due to destruction of shrubs and saplings, which, if maturing, could cause the decay of *F. exsecta* nests by increasing shadow (Seifert 2000).

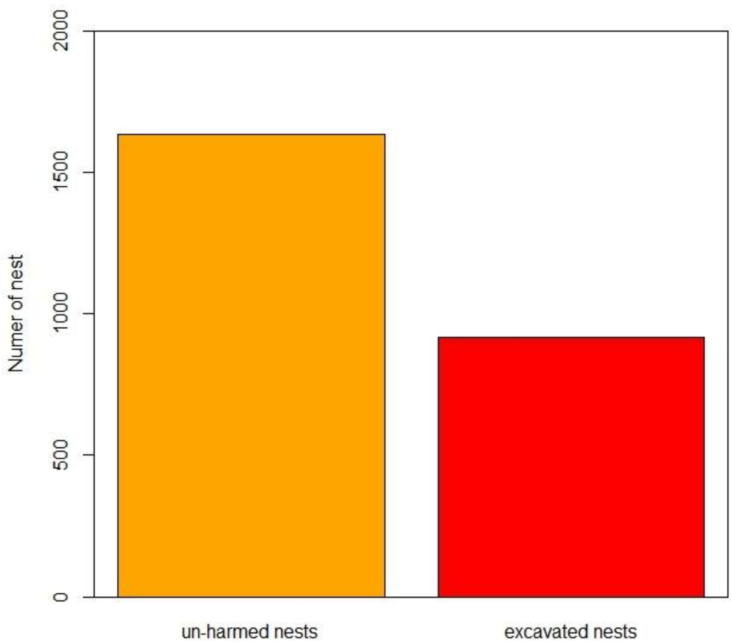

Fig. 13. *Number of unharmed and bear-excavated Formica exsecta nests.*

5 Conclusions

Our findings have important implications for our understanding of supercoloniality in ants.

- Our most studied *F. exsecta* supercolony is by far the largest known European polydomous system not just for this species, but most probably for all mound building territorial *Formica* species. The entire population is remarkably large; it could well be one of the largest *F. exsecta* populations in Europe, which implies the need for its protection.

- The *F. exsecta* population presented here seems extremely healthy and stable due to high ant nest density and ant nest number, which can be caused both by the stability of permanent food sources, as e.g., aphid colonies.

- *F. exsecta* polydomous systems develop in grazed habitats, open areas with low shrub-coverage and reduced shrub height. The traditional low intensity grazing controls the height and cover of shrubs, thus prevents the development of forests, which are un-habitable for *F. exsecta*. Thus, to some extent, grazing by cows could be beneficial for *F. exsecta* supercolonies, as it could keep trees and shrubs below a certain height. The features (no. of nests, nest density, nest size) of the studied polydomous systems are unique in Europe, which shows that the habitat conditions are optimal for *F. exsecta*.

- The lack of differences in the frequency and duration of peaceful mutual investigation by antennation between ants from different nests might be caused by small differences in colony odor. This study supports that our study system can indeed function as a supercolony, since there is a mutual acceptance among ants coming from various parts of the same system, but they are even tolerant to workers from different system of the same population. The results are also supported by the lack of aggression towards each other, but also by the high level of aggression towards alien rivals as *F. sanguinea*.

- The lethal endoparasitic fungus *Pandora myrmecophaga* is known from the studied *Formica exsecta* polydomial system. We tested the hypothesis regarding the existence of simple defense mechanism: workers would dispose of every corpse, as potential source of infection, appearing on grass-blades, thus lowering the chances of spore dispersal. After discovering the corpses ants removed them quickly, and larger nests, which were more active, reacted generally more promptly. The result of this efficient reaction is the prevention of the development of the conidia, which needs at least 2-4 days in natural conditions, but in favorable conditions, with elevated temperature and moisture the spores could develop after one day (pers. obs.). The generality of this prophylactic strategy is very important, since usually specific defense mechanisms are costly to maintain.

- The consumption of pollen in ants can be much more frequent than originally thought. In suboptimal circumstances ants could exploit this resource too. In an area dominated by territorials as the supercolonial *F. exsecta* and *F. polyctena* the co-occurring submissive species, as *Myrmica* spp., *Temnothorax* spp. and *Serviformica* spp. used more frequently pollen as alternative food source, so pollen constitutes an important resource in such a habitat, where the competition is fiercer. This also underlines the importance of repellent agents produced by plants, since our study demonstrates that in the lack of these agents ants might easily turn to utilize this alternative food source and thus heavily exploit plants.

- Our large *F. exsecta* supercolony constitutes an important food source for brown bears in the area. It is not clear though, whether bear attacks could actually be fatal to the *F. exsecta* supercolony on the long run. Regular bear visits of the meadow may, in a strange way, even benefit the supercolony due to destruction of shrubs and saplings, which, if maturing, could cause the decay of *F. exsecta* nests by increasing shadow.

- The recent changes in Romanian agriculture, which have caused a drastic decrease in cow numbers and consequently abandonment of traditional extensive grazing and haymaking techniques, additionally the spread of illegal burning as management strategy, may endanger the survival of this unique population on the long run. Thus, only the implementation of an appropriate management plan could help the survival of this intriguing social system with its unique features.

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8 List of scientific publications from the topic of the thesis

Erős K, Markó B, Rákosy L (2015) Simple defence mechanisms that keep Pandora's box closed in an ant nest system parasitized by a highly pathogenic fungus. PLoS One (*submitted*).

Erős K, Markó B (2015) A peculiar natural disturbance factor for supercolonies: brown bears (*Ursus arctos*). Ursus (*submitted*)

Erős K, Markó B, Szabó Á (2015) Pollen as alternative food source for subdominant ant species in suboptimal circumstances on the territories of polydomous *F. exsecta* (*manuscript*).

Erős K, Markó B, Babik H, Ślipiński P, Czechowski W (2015) Pollen as alternative food source for subdominant ant species in suboptimal circumstances on the territories of polydomous *F. polyctena* (*manuscript*).

Csata E, Czekes Zs, Erős K, Német E, Hughes M, Csősz S, Markó B (2013) Comprehensive survey of Romanian myrmecoparasitic fungi: new species, biology and distribution. North-Western Journal of Zoology 9 (1): 23-29. *IF: 0.747*

Csata E, Markó, B., Erős K, Gál Cs, Szász-Len A-M, Czekes Zs (2012) Outstations as stable meeting points for workers from different nests in a polydomous nest system of Formica exsecta NYL. (Hymenoptera: Formicidae). Polish Journal of Ecology 60(1): 177-186. *IF: 0.506*

Markó B, Czekes Zs, Erős K, Csata E, Szász-Len A-M (2012) The largest known polydomous system of mound building Formica ants (Hymenoptera: Formicidae) in Europe. North-Western Journal of Zoology 8(2): 287-291. *IF: 0.747*

Erős K, Csata E, Gál Cs, Czekes Zs, Szász-Len A-M, Szőke Zs, Maák I, Markó B (2011) Hangya-levéltetű-gazdanövény kapcsolatok egy egyedi szuperkoloniális rendszerben a vaslábi Fenékláp határában (Ant-aphid-host plant relationships in a unique polydomous system near the protected După Luncă area at Voşlobeni). In: Markó, B., Sárkány-Kiss, E. (ed.): A Gyergyói-medence: egy mozaikos táj természeti értékei. Presa Universitară Clujeană, Cluj-Napoca p. 244: 131-148 pp.

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9 Other scientific publications

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