

CLOSE NESTING ASSOCIATION OF TWO ANT SPECIES
IN ARTIFICIAL SHELTERS:
RESULTS FROM A LONG-TERM EXPERIMENT

LÁSZLÓ GALLÉ, ORSOLYA KANIZSAI, ISTVÁN MAÁK and GÁBOR LÓRINCZI

Department of Ecology, University of Szeged
H-6726 Szeged, Közép fasor 52, Hungary; E-mail: galle@bio.u-szeged.hu

Close nesting (real or quasi plesiobiosis) is the simplest form of spatial associations of heterospecific ant colonies that share the same microhabitat, but remain separate as individual units. We studied the tendency to close nesting between two ant species, *Lasius psammophilus* and *Plagiolepis taurica*, under slate plates used as artificial nesting sites during a 34 years long study period. 2410 nest records of 11 ant species were made under the plates, and a total of 181 close nesting associations were observed, most of which between *L. psammophilus* and *P. taurica*. The hypothesis of the weak antagonism between the two species was supported by (1) the rate of nesting associations, which was lower than expected from random probabilities; (2) the maximum of the index of avoidance, at intermediate densities; (3) the negative relationship between the unoccupied nesting shelters and the frequency of close nesting; (4) the tendency of individual and group level avoidance and (5) the low rate of interspecific aggression. The benefit of choosing favorable nesting sites and the risk of interspecific competition are in trade-off relation and the attractiveness of nesting shelters is the stronger constraint; therefore it can be regarded as the primary driver of the formation of spatial associations between the colonies of the two studied species.

Key words: ants, plesiobiosis, competition, *Lasius psammophilus*, *Plagiolepis taurica*.

INTRODUCTION

Close nesting (plesiobiosis, sensu KANIZSAI *et al.* 2013) is the most primitive form of spatial associations of heterospecific ant colonies. By definition, colonies of plesiobiotic partners share the same microhabitat without strong interdependence or communication between each other. Plesiobiotic nests are either adjacent to one another, e.g. with common walls (real plesiobiosis) or are in their close vicinity (10–50 cm distance, quasi plesiobiosis) but always remain separate as individual units, and the heterospecific colonies do not mix (HÖLLDOBLER & WILSON 1990). In most of the documented cases, however, no evidence is given for the absence of interactions.

Although the term plesiobiosis was established in 1901 by WHEELER (1901), and several cases were demonstrated already by the mid-1940s (MORLEY 1945, 1946), its research history is not too extensive (see reviewed by KANIZSAI *et al.* 2013).

In this paper we describe the changes in the frequency of plesiobiotic associations between two species, *Lasius psammophilus* and *Plagiolepis taurica* (a species pair that has not been described as plesiobiotic partners in other studies)

as a function of the changes in the density of nests in artificial nesting sites in a 34 years long study period.

Two main external factors are usually considered as playing a role in the initiation of plesiobiotic associations in ants: the scarcity of suitable nesting sites (CZECHOWSKI 2004a) as a forcing factor, and the appropriate amount of available food sources, which contributes to higher nest densities (KANIZSAI *et al.* 2013). These factors represent essentially two sides of the same coin: the scarcity of nesting sites can be a consequence of high nest density brought about by rich food supply.

If we do not postulate the absence of intercolonial interactions, three concurrent hypotheses can be set up on the constraints or conditions determining the frequency of plesiobiotic associations:

(1) Positive relationship (e.g., mutualism) exists between the potential plesiobiotic partners, besides same microhabitat preference, therefore they attract each other to the same nesting site. In this case the frequency of plesiobiotic associations is higher than expected from the random occupation of the available nesting sites.

(2) Neutralism: no interactions or one-sided effects exist between the species and the frequency of plesiobiosis is more or less the same as expected from random distribution.

(3) Negative interspecific relationships (competition or other types of repellent effects). In this case the cost of occupying suitable nesting sites is the tolerance of the presence of a hostile species. This hypothesis can be divided into two parts: (a) Strong interspecific antagonism (e.g., intense aggressiveness), which prevents plesiobiosis, and we can interpret it as a background of the minimal rate or absence of close nesting; and (b) weak antagonism, which can also lead to a lower rate of close nesting than expected by the neutral hypothesis, but does not exclude it. In this case, the maximal differences between the expected and observed frequencies are presumed at intermediate nest densities, because at too low densities the theoretical probability of plesiobiosis is also low, while at very high densities, in the absence of available free nesting sites, the co-occurring species cannot avoid joint nesting to gain preferable nesting shelters.

Our aim in this study was to investigate the frequency and the density dependence of close nesting, and to test the validity of the above hypotheses.

MATERIAL AND METHODS

The study was conducted on a sandy grassland near the village of Bugacpusztaháza in the Kiskunság National Park, central Hungary (N 46°41'49.3" E 19°36'10.5"). The typical landscape type of this region is forest-steppe, consisting of solitary trees, smaller or larger patches of forests surrounded by grasslands, where dead twigs, barks and logs fallen from trees are utilized as nesting shelters by both forest and grassland ants. The particular study

site is made up of small dunes up to 3 m high with very dry soil, and between-dune slacks with a bit more humid soil and denser vegetation. A 2.4 ha plot was isolated by fencing in 1976 to exclude grazing and other types of disturbance regimes. As a result of isolation, a secondary succession process started from grazing conditions to a semi natural stage of the vegetation. For the present study a dune ridge and a slack were selected where the vegetation succession was in the final grassland stage without trees and natural shelters. The vegetation on the dune ridge is open grassland (*Festucetum vaginatae* association) predominated by *Festuca vaginata*, *Stipa borysthenica*, *Euphorbia seguieriana*, *Dianthus serotinus* and in dryer years *Stipa capillata* and *Secale sylvestre*. The slack is covered by *Molinia hungarica*, dwarf *Salix repens rosmarinifolia* bushes, *Festuca pseudovina* and *Potentilla arenaria* (*Molinio-Salicetum rosmarinifoliae* formation).

In 1981 a total of 40 slate plates with a size of 40 × 40 × 0.3 cm were placed on a dune top and also 40 plates in a dune slack, and left there until 2014. During this period only the broken ones were replaced. The plates were arranged in a grid and the distance between adjacent plates was 50 cm; therefore an ant colony could easily reach and occupy one of them. Ants colonized the underside of the plates in spring and in a lesser extent also in autumn, because the temperature under them exceeded that of the ambient soil (e.g., the mean difference was 13.18±3.96 °C on the sand dune and 16.02±3.27 °C in the dune slack on 29th April, 2013, and 5.43±1.24 °C on the sand dune, and 9.55±4.00 °C in the dune slack on 15th May, 2013). The differences were significant in all cases (Student's t-test, $p < 0.0001$). As the temperature under the plates was too high in summer, ants left them and recolonized again either in autumn or in the next spring after overwintering deep in the soil. The ant colonies presumably survived for years and new ones were established during the study period. As the ants left and re-occupied the plates once or twice every year and new temporary plesio-biotic associations started again in this way, the observations of plesio-biosis were not affected by pseudoreplication.

The size of the plates was small enough to observe small scale nesting associations, real or quasi plesio-biosis, because when colonized by more than one nest, the maximum distance between the nearest nest borders did not exceed 25 cm, as a rule.

We laid altogether 43 smaller plates with sizes of 20 × 20 × 0.3, 15 × 15 × 0.3 and 10 × 10 × 0.3 cm with 50 cm distance, too, in 2014, to ascertain how the frequency of close nesting (in this case: real plesio-biotic) associations changes with different shelter size.

We made a total of 41 observations during the 34 years of the study period. The colonies were identified and counted by lifting the plates, which caused only a slight disturbance without destroying the nests. We regarded colonies as the groups of individuals with nest galleries, entrances and/or brood. Because of technical reasons, there was no census in some years, while in certain years more than one observation was performed at different occupation rates. During the observations we identified the ant species occupying the plates and counted the number of their nests under each plate. During the 3323 individual plate observations we recorded a total of 2432 ant nests, providing a sufficient data set to perform the evaluation at least for the most frequent species.

Interspecific aggressiveness is one of the frequent mechanisms of negative relationships between ant species. We conducted pairwise aggression tests between workers of heterospecific colonies in 90 × 32 mm transparent plastic vials in 2013 and 2014. In average, 9.3 (minimum 5 and maximum 18) individuals from each tested plesio-biotic colony were put into vials and their behaviour was observed with a magnifier lens for 5 minutes. When encounters were detected, we scored the response of ants using a three degree aggression scale: (1) escaping, i.e. the submissive ("weaker") worker escapes by running away; (2) threatening (intensive investigation usually with open mandibulae) and (3) attacking

Table 1. The total number of ant nests under the plates of 40 × 40 cm size and the absolute frequency of plesiobiotic associations.

Species	Number of nests	In plesiobiotic association
<i>Myrmica schencki</i> Viereck, 1903	1	0
<i>Solenopsis fugax</i> (Latreille, 1798)	1	0
<i>Tetramorium</i> cf. <i>caespitum</i> (Linnaeus, 1758)	284	22
<i>Tapinoma subboreale</i> Seifert, 2012 ¹	66	8
<i>Plagiolepis taurica</i> Santschi, 1920	717	165
<i>Lasius niger</i> (Linnaeus, 1758)	78	4
<i>Lasius psammophilus</i> Seifert, 1992	1165	154
<i>Lasius paralienus</i> Seifert, 1992	2	0
<i>Lasius carniolicus</i> Mayr, 1861	2	0
<i>Formica sanguinea</i> Latreille, 1798	13	2
<i>Formica cunicularia</i> Latreille, 1798	63	7

¹Given as *Tapinoma madeirense* Forel, 1895 in the recent checklist of Hungarian ants (Csősz *et al.* 2011).

aggressively (biting, hanging on the other's tarsus). A total of 1854 potential encounters between heterospecific individuals were tested.

In most cases, the traditional statistics (product-moment correlation, regression analysis, Chi-square test, Student's t) were sufficient for data evaluation (further details are given in results section). Besides, we employed an index of avoidance to investigate the segregation tendency of heterospecific ant colonies at different densities: $IA = (E_i - O_i) / E_i$ where E_i is the expected number of plesiobiotic associations calculated from the probabilities of co-occurrences assuming that colonization is a random process, and O_i is the observed frequency at the i th count. This index is similar to the "C-score" index of checkerboard distribution (STONE & ROBERTS 1990, GOTELLI 2000, GIBB & PARR 2010), but applicable at changing densities, which is the case in the present study.

RESULTS

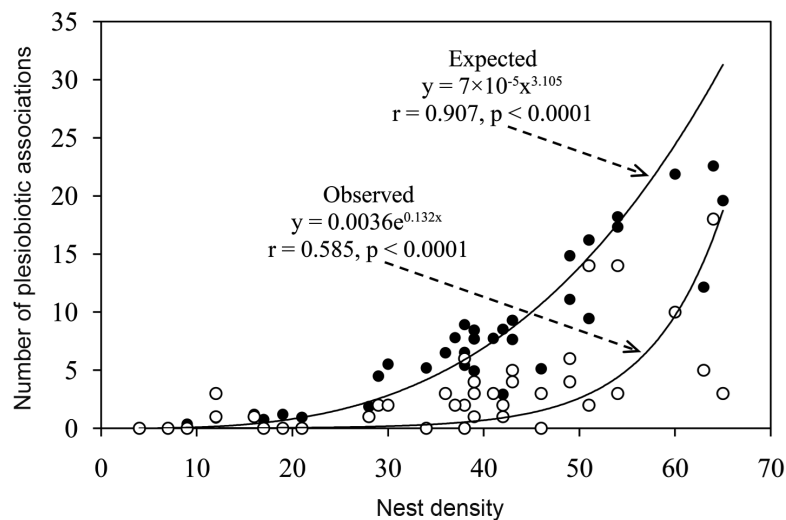
We carried out a total of 2392 nests records of 11 ant species under the plates of 40 × 40 cm size (Table 1) and 40 nest records under smaller plates in 3 observations in 2014. The two absolute predominant species, *Lasius psammophilus* and *Plagiolepis taurica* occurred on the dune top in the first part of the study period, while *Tetramorium* cf. *caespitum*, *Lasius niger*, *Tapinoma subboreale*, *Formica sanguinea*, *Myrmica schencki* and *Lasius paralienus* were observed only in the dune slack. Later on, *L. niger*, *F. sanguinea* and *M. schencki* gradually disappeared, while *L. psammophilus* and *P. taurica* established nests in the slack as well, presumably as a consequence of regional climate change (GALLÉ pers. obs., GALLÉ *et al.* in prep.).

Table 2. The number of observed plesiobiotic associations according to the participating species.

	<i>L. niger</i>	<i>F. sanguinea</i>	<i>F. cunicularia</i>	<i>T. subboreale</i>	<i>T. cf. caespitum</i>	<i>P. taurica</i>	<i>L. psammophilus</i>
<i>L. psammophilus</i>	0	0	0	0	4	150	x
<i>P. taurica</i>	0	0	1	6	8	x	
<i>T. cf. caespitum</i>	4	0	6	0	x		
<i>T. subboreale</i>	0	2	0	x			
<i>F. cunicularia</i>	0	0	x				
<i>F. sanguinea</i>	0	x					
<i>L. niger</i>	x						

We recorded a total of 181 close double nesting associations. No triplets were found. The species-level absolute frequency of plesiobiotic associations (Table 1) correlated well with the density of the nests of the species (product-moment correlation $r = 0.956$, $p < 0.0001$), while its relative frequency (plesiobiotic nests/all nests) did not ($r = 0.536$, $p > 0.1$). In most cases (94.73%) the frequencies of observed plesiobiotic associations were smaller than expected from the theoretical probability of the joint occurrences (Fig. 1).

150 (82.9%) of the total 181 recorded plesiobiotic associations were between *L. psammophilus* and *P. taurica* (Table 2), providing the only data set satisfying the conditions for further evaluation. As the nests of both *L. psam-*

**Fig. 1.** The observed and expected number of plesiobiotic associations between heterospecific colonies as a function of the total number of ant nests under the slate plates.

mophilus and *P. taurica* occurred on the top of the sand dune with high density during the whole study period, we restricted hereafter the scope of our analyses on the two species to the data from this habitat, where the mean nest density of *L. psammophilus* and *P. taurica* was 0.67 and 0.27 nest/plate, respectively. As *L. psammophilus* was the most common species, we calculated the occupation rate of the shelters from the number of plates colonized by this species.

We found a negative correlation between the relative frequency of plesiobiotic associations of *P. taurica* and the *psammophilus*-free sites (Fig. 2), indicating a tendency of mutual or one-sided avoidance between the two species.

The index of avoidance as a function of the nest density of *L. psammophilus* fits the equation $y = -0.0008x^2 + 0.059x - 0.35$ ($r = 0.48$, $p = 0.01$), which has a maximum at intermediate density (37 nests, the maximum density was 54 for the 80 plates in total).

We found no difference in the rate of occupation between the 40 × 40 cm and two categories of the smaller plates (20 × 20 and 15 × 15 cm, $p = 0.14$ and 0.37, respectively, Chi-square test). The smallest ones, however, were colonized at significantly lower rate ($p = 0.012$). No heterospecific joint nesting was observed under the smaller plates of any category.

During the aggression tests, there was a segregation tendency between the workers of the two species in the vials as a group level reaction. Conspecific workers recruited to different parts, e.g., to the opposite ends of the vials in 82% of the tests. Workers of the two different species tried to avoid encounters at low rates. *P. taurica* avoided *L. psammophilus* workers in 23.8% of the tests

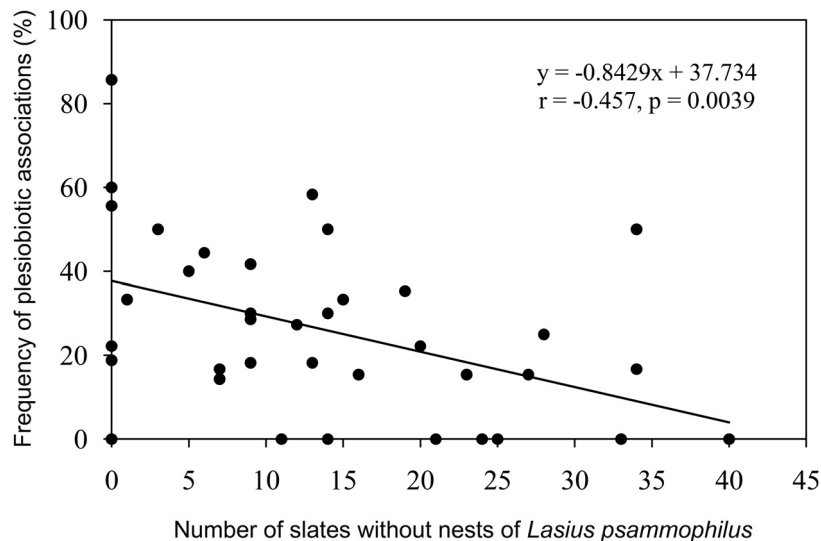


Fig. 2. The relationship between the frequency of plesiobiotic associations between *Lasius psammophilus* and *Plagioteles taurica* and the number of plates without nests of *L. psammophilus*.

Table 3. The total number and the relative frequency of elements of behaviour between *L. psammophilus* (LAPS) and *P. taurica* (PLTA) in the aggression tests. The arrows show the species with submissive behaviour.

All possible encounters: 1854				Relative %	Total	%
Type of interaction	LAPS→ PLTA	PLTA→ LAPS	LAPS→ PLTA	PLTA→ LAPS		
1. Escaping	53	15	2.86	0.81	68	3.61
2. Threatening	4	0	0.2	0.00	4	0.21
3. Attacking	6	4	0.32	0.21	10	0.54
Total					82	4.42

and this tendency was mutual in 4.8%. The proportion of individual-level negative interactions can be considered low (Table 3) as we observed 82 such cases (4.42%) and real aggression (level 3) was detected in only 10 of them (0.54%).

DISCUSSION

A reasonable question is whether the plates were really attractive for the ants or the nests occurred under them only by chance, with the same probability as in any other part of an identical area in the same habitat. We did not estimate the density of nests among the plates during the study period to avoid intensive disturbance by soil excavation. As former nest density estimates via excavation showed, the mean density of the nests of *L. psammophilus* was 1.1 nest/m², while that of *P. taurica* was 0.3 nest/m² in the neighbouring parts of the same habitat (GALLÉ 1980, using the former names *Lasius alienus* Foerster and *Plagiolepis vindobonensis* Lomnicki). These are much lower values than the densities of nests under the plates (7.04 nest/m² for *L. psammophilus* and 1.92 nest/m² for *P. taurica*, respectively) when only the area of plates is considered, and the overlap between the distributions of the two data sets was only 5.26% for *L. psammophilus* and 0.00% for *P. taurica*. Relating the number of ant nests censused under the plates to the whole area of the plot where plates were used, we obtained 0.9 nest/m² and 0.36 nest/m² mean densities for *L. psammophilus* and *P. taurica*, respectively, which is comparable to the figures by GALLÉ (1980), meaning that the majority of the nests were under plates. In addition, former grid-samplings and nest mappings showed that the minimal distance between the nest centers of *L. psammophilus* and *P. taurica* always exceeded 0.5 m (GALLÉ 1979), whereas the distances under the plates were smaller in all cases. Therefore we can conclude that there is a tendency of aggregation under the plates, although both species, being typical of sandy grasslands, can survive without shelters. However, the too small size of the shelters limits the probability of occupation and close nesting.

Another problem is the size and the structure of colonies. In particular, the polydomous species, *L. psammophilus* establishes large colonies, the stations of which can occupy several nesting sites (NIELSEN 1972, GALLÉ 1979, 1980). The fine-scale pattern analysis based on Lloyd's patchiness index (LLOYD 1967) indicated an aggregation of the nest entrances of *L. psammophilus* at 1–3 m² in the same grassland (GALLÉ *et al.* 1994), which could correspond to the size of the nests, and on this basis we cannot exclude the possibility that a single colony of *L. psammophilus* could have occupied more plates. However, on the basis of the results by former density estimations with nest excavation (GALLÉ 1978, 1980, 1991), it is unlikely that *L. psammophilus* established brood chambers in more than one shelter. Therefore, the number of plates with the presence of brood or exuvia of pupae could well correspond to the number of nests of *L. psammophilus*. On the other hand, regarding *T. cf. caespitum* and *Formica* species, it was clear that a single colony occupied two, three or even more plates in the dune slack of the studied habitat.

So far, 49 species have been documented in plesiobiotic associations in the literature, and 29 of them belong to the subfamily Formicinae (a complete list is given by KANIZSAI *et al.* 2013). No data regarding plesiobiosis is known on either species studied here, nor on *L. alienus* and *P. vindobonensis*, which were partly the former names of *L. psammophilus* and *P. taurica* (SEIFERT 1992, Csósz *et al.* 2011). As both species belong to Formicinae, the number of recorded cases has risen to 31, and, in addition, we found plesiobiotic colonies of *Tapinoma subboreale*, too (Table 1), so the total number of species has increased to 52. More than half of the observed cases of plesiobioses were recorded in Finland and Poland, due to the intensive myrmecological researches in these countries (CZECHOWSKI 2002, 2003, 2004a, b, 2005, CZECHOWSKI & CZECHOWSKA 2000, CZECHOWSKI & VEPSÄLÄINEN 1999, WŁODARCZYK *et al.* 2009). *P. taurica*, a species of southern distribution in Europe, does not occur in these countries; therefore its participation in a plesiobiotic relationship could not be documented by the former authors.

The rate of plesiobiosis that was lower than expected from random probabilities, the maximum of the index of avoidance at intermediate densities, the negative relationship between the unoccupied nesting shelters and the frequency of plesiobiosis, the tendency of individual and group level avoidance, and the low rate of interspecific aggression support the validity of the weak antagonism sub-hypothesis (3b outlined in the introduction) between *L. psammophilus* and *P. taurica*. The presence of competition, the niche differences and niche shifts between the populations of the two species have already been documented by GALLÉ (1986), who found that *L. psammophilus* was always the dominant competitive partner. In the present study we found a low rate of interspecific aggression by *P. taurica*, too. As the tested workers were collected

from the nests, this behaviour could be a nest-defence aggression and differs from that studied by GALLÉ (1986) earlier, outside the nests.

Concerning the benefit of choosing favorable nesting sites and the risks of interspecific competition, the former one is the stronger constraint and it can be regarded as the prime driver of the formation of plesiobiotic associations between the colonies of *L. psammophilus* and *P. taurica*. The role of habitat type and structure is undoubtedly an important component from among the background factors and driving forces of plesiobiosis listed by KANIZSAI *et al.* (2013) and natural shelters are essential elements of the habitat structure for ants. Sandy grasslands are typical components of the forest-steppe landscapes in the Kiskunság region of Central Hungary, where natural shelters are dead twigs, barks and logs originated from the single trees and the neighbouring forest patches.

The spatial arrangement of populations is an important chapter in ecology (TILMAN & KAREIVA 1997, FORTIN & DALE 2005). Beside the physical properties of habitats, two main factors are generally considered to lead to a particular spatial configuration, namely the patterns of colonization and the degree of competition. The trade-off between these constraints has long been suggested and demonstrated, its research dates back to the 1950s (HIGGINS & CAIN 2002, KNEITEL & CHASE 2004). This topic has been studied on larger, habitat and metapopulation scales in several theoretical and case investigations (e.g., HANSKI 1999, YU & WILSON 2001, HIGGINS & CAIN 2002, LEIBOLD & MILLER 2004, SEIFAN *et al.* 2013). In the present study, however, we employed a finer scale approach, where the relation between the benefit of choosing favorable nesting sites and the risk of interspecific competition can be interpreted as a special case of trade-offs. In this case, the occupation of nesting shelters replaces the colonization, which has been investigated on larger scales in previous studies.

A large number of papers have documented trade-off relations in ants (LACH *et al.* 2010). In studies using a similarly fine scale approach as the one in the present study, FELLERS (1987) and subsequent authors (see PARR & GIBB 2010) described discovery-dominance trade-offs, but in a different context. PARR and GIBB (2012) found little empirical support for discovery-dominance trade-offs from a meta-analysis and their own field works. Evidence, however, for dominance *versus* thermal tolerance trade-off has been demonstrated in ant communities (CERDÁ *et al.* 1997, BESTELMEYER 2000, LESSARD *et al.* 2009). STANTON *et al.* (2002) reported a small-scale competition-colonization trade-off in a guild of African acacia-ants, with strong competition for nesting sites of better quality. ADLER *et al.* (2007) synthesized these two approaches with extending the models of the competition-colonization trade-off to the dominance-discovery trade-offs.

As the competition between the populations of *Plagiolepis taurica* and *Lasius psammophilus* is not only for preferable nesting sites, but also for other resources in other dimensions, where *L. psammophilus* proved to be dominant (GALLÉ 1986), we agree SEIFAN *et al.* (2013) that the simple and popular dichotomous trade-off approaches are not sufficient to explain community patterns.

*

Acknowledgements – This study is a part of the long term Bugac Project. When our investigations started, László Móczár was the leader of our department. We would like to congratulate professor Móczár on his 100th birthday with this paper. The Directorate of Kiskunság National Park has provided safe and undisturbed research site for decades and gave financial support, too. Our research was also sponsored by different grants of the Hungarian Scientific Research Found, the Hungarian Academy of Sciences and the Hungarian Ministry of Environment. We thank Csaba Németh for his technical help and Csaba Tölgyesi for improving the English style of our manuscript.

REFERENCES

- 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. *The American Naturalist* **169**: 323–333.
- BESTELMEYER, B. T. (2000) The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. *Journal of Animal Ecology* **69**: 998–1009.
- CERDÁ, X., RETANA, J. & CROS, S. (1997) Thermal disruption of transitive hierarchies in Mediterranean ant communities. *Journal of Animal Ecology* **66**: 363–374.
- CsÓSZ, S., MARKÓ, B. & GALLÉ, L. (2011) The myrmecofauna (Hymenoptera: Formicidae) of Hungary: an updated checklist. *North-Western Journal of Zoology* **7**: 55–62.
- CZECHOWSKI, W. (2002) Plesiobiosis between *Formica fusca* L. and wood ants (Hymenoptera, Formicidae) as a sign of nest competition. *Przeгляд Zoologiczny* **46**: 81–86.
- CZECHOWSKI, W. (2003) Plesiobiosis between *Formica fusca* L. and *Myrmica rubra* (L.) (Hymenoptera, Formicidae). *Przeгляд Zoologiczny* **47**: 115–118.
- CZECHOWSKI, W. (2004a) Scarcity of sites suitable for nesting promotes plesiobiosis in ants (Hymenoptera: Formicidae). *Entomologica Fennica* **15**: 211–218.
- CZECHOWSKI, W. (2004b) Plesiobiosis between dendrophilous ants: *Camponotus fallax* (F.) and *Lasius brunneus* (Latr.) (Hymenoptera, Formicidae). *Przeгляд Zoologiczny* **48**: 201–205.
- CZECHOWSKI, W. (2005) Nest competition between *Camponotus vagus* (Scopoli, 1763) and *Camponotus herculeanus* (Linnaeus, 1758) (Hymenoptera: Formicidae) in Białowieża Forest (Poland). *Myrmecological News* **7**: 43–45.
- CZECHOWSKI, W. & VEPSÄLÄINEN, K. (1999) Plesiobiosis between *Formica fusca* L. and *Formica aquilonia* Yarr. (Hymenoptera, Formicidae). *Annales Zoologici* **49**: 125–127.
- CZECHOWSKI, W. & CZECHOWSKA, W. (2000) *Formica cinerea fuscocinerea* For. in the Pieniny Mts, its untypical habitat and plesiobiosis with *Lasius flavus* (F.) (Hymenoptera, Formicidae). *Fragmenta Faunistica* **43**: 131–133.
- FELLERS, J. H. (1987) Interference and exploitation in a guild of woodland ants. *Ecology* **68**: 1466–1478.

- FORTIN, M. J. & DALE, M. (2005) *Spatial analysis. A guide for ecologists*. Cambridge University Press, Cambridge, 365 pp.
- GALLÉ, L. (1978) Dispersion of the nests of an ant species (Hymenoptera: Formicidae). *Acta Biologica Szegediensis* **24**: 105–109.
- GALLÉ, L. (1979) Formicoidea populációk denzitása és produktivitása gyepcönözisokban (Density and productivity of grassland ants). PhD Thesis, University of Szeged, 125 pp. [in Hungarian]
- GALLÉ, L. (1980) Dispersion of high density ant populations in sandy soil grassland ecosystems. *Acta Biologica Szegediensis* **26**: 129–135.
- GALLÉ, L. (1986) Habitat and niche analysis of grassland ants. *Entomologia Generalis* **11**: 197–211.
- GALLÉ, L. (1991) Structure and succession of ant assemblages in a north European sand dune area. *Ecography* **14**: 31–37.
- GIBB, H. & PARR, C. L. (2010) Co-occurrence analyses: what are they and how are they work? Pp. 86–87. In: LACH, L., PARR, C. L. & ABBOTT, K. L. (eds): *Ant ecology*. Oxford University Press, Oxford.
- GOTELLI, N. J. (2000) Null model analysis of species co-occurrence patterns. *Ecology* **81**: 2606–2621.
- HANSKI, I. (1999) *Metapopulation ecology*. Oxford University Press, Oxford, 313 pp.
- HÖLLDOBLER, B. & WILSON, E. O. (1990) *The ants*. Harvard University Press, Cambridge, 732 pp.
- HIGGINS, S. L. & CAIN, M. L. (2002) Spatially realistic plant metapopulation models and the colonization–competition trade-off. *Journal of Ecology* **90**: 616–626.
- KANIZSAI, O., LŐRINCZI, G. & GALLÉ, L. (2013) Nesting associations without interdependence: A preliminary review on plesiobiosis in ants. *Psyche* **2013**: 1–9.
- KNEITEL, J. M. & CHASE, J. M. (2004) Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters* **7**: 69–80.
- LEIBOLD, M. A. & MILLER, T. E. (2004) From metapopulations to metacommunities. Pp. 133–150. In: HANSKI, I. & GAGGIOTTI, O. E. (eds): *Ecology, genetics and evolution of metapopulations*. Elsevier Academic Press, Burlington–San Diego–London.
- LESSARD, J. P., DUNN, R. R. & SANDERS, N. J. (2009) Temperature-mediated coexistence in temperate forest ant communities. *Insectes Sociaux* **56**: 149–156.
- LLOYD, M. (1967) 'Mean crowdin'. *Journal of Animal Ecology* **36**: 1–30.
- MORLEY, D. W. (1945) Observations on some plesiobiotic colonies of ants (Hymenoptera), with notes on some other mixtobiotic colonies. *Proceedings of the Royal Entomological Society of London* **20**: 1–4.
- MORLEY, D. W. (1946) The interspecific relations of ants. *Journal of Animal Ecology* **15**: 150–154.
- NIELSEN, M. G. (1972) An attempt to estimate energy flow through a population of workers of *Lasius alienus* (Först.) (Hymenoptera: Formicidae). *Natura Jutlandica* **16**: 97–107.
- PARR, C. L. & GIBB, H. (2010) Competition and the role of dominant ants. Pp. 77–96. In: LACH, L., PARR, C. L. & ABBOTT, K. L. (eds): *Ant ecology*. Oxford University Press, Oxford.
- PARR, C. L. & GIBB, H. (2012) The discovery-dominance trade-off is the exception rather than the rule. *Journal of Animal Ecology* **81**: 233–241.
- SEIFAN, M., SEIFAN, T., SCHIFFERS, K., JELTSCH, F. & TIELBÖRGER, K. (2013) Beyond the competition-colonization trade-off: Linking multiple trait response to disturbance characteristics. *The American Naturalist* **181**: 151–160.

- SEIFERT, B. (1992) A taxonomic revision of the Palaearctic members of the ant subgenus *Lasius* s. str. (Hymenoptera: Formicidae). *Abhandlungen und Berichte des Naturkundemuseums Görlitz* **66**: 1–67.
- SEIFERT, B. (2012) Clarifying, naming and identification of the outdoor species of the ant genus *Tapinoma* Förster, 1850 (Hymenoptera: Formicidae) in Europe north of the Mediterranean region with description of a new species. *Myrmecological News* **16**: 139–147.
- STANTON, M. L., PALMER, T. M. & YOUNG, T. P. (2002) Competition–colonization trade-offs in a guild of African acacia-ants. *Ecological Monographs* **72**: 347–363.
- STONE, L. & ROBERTS, A. (1990) The checkerboard score and species distribution. *Oecologia* **85**: 74–79.
- TILMAN, D. & KAREIVA, P. (1997) *Spatial ecology. The role of space in population dynamics and population interactions*. Princeton University Press, Princeton, 368 pp.
- VANTAUX, A., DEJEAN, A., DOR, A. & ORIVEL, J. (2007) Parasitism versus mutualism in the ant-garden: parabiosis between *Camponotus femoratus* and *Crematogaster levior*. *Insectes Sociaux* **54**: 95–99.
- WHEELER, M. W. (1901) The compound and mixed nests of American ants. *The American Naturalist* **35**: 1007–1016.
- WŁODARCZYK, T., ZMIHORSKI, M. & OLCZYK, A. (2009) Ants inhabiting stumps on clearcuts in managed forest in Western Poland. *Entomologica Fennica* **20**: 121–128.
- YU, D. W. & WILSON, H. B. (2001) The competition–colonization trade-off is dead. Long live the competition–colonization trade-off. *The American Naturalist* **158**: 49–63.

Revised version received May 19, 2014, accepted October 6, 2014, published November 12, 2014