Myrmecological News	12	171-181	Vienna, September 2009

Effects of the invasive garden ant, *Lasius neglectus* VAN LOON, BOOMSMA & ANDRÁSFALVY, 1990 (Hymenoptera: Formicidae), on arthropod assemblages: pattern analyses in the type supercolony

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Abstract

Invasive ant species represent a serious threat to many ecological communities, often causing decreases in the abundance, species richness and diversity of native ants and other arthropods. The invasive garden ant, *Lasius neglectus* VAN LOON, BOOMSMA & ANDRÁSFALVY, 1990, is an invasive tramp species that forms dense supercolonies. We studied the ecological impacts of the type supercolony of this species on other ants and surface-active arthropods in Budatétény, Budapest, Hungary. Arthropod abundance, species richness and diversity were estimated by using pitfall traps.

The *L. neglectus* supercolony radically changed the composition of the arthropod assemblage. The diversity of total arthropods, Coleoptera and other Formicidae was lower in the areas with *L. neglectus* supercolony than in the control areas. The presence of *L. neglectus* caused a significant reduction in species richness of Isopoda and other Formicidae, but a significant increase in Hemiptera.

Lasius neglectus had a significant negative effect on the abundance of the arthropod species *Armadillidium vulgare* (LATREILLE, 1804) (Isopoda: Armadillidiidae), *Trachelipus rathkii* (BRANDT, 1833) (Isopoda: Trachelipodidae), *Harpalus rubripes* (DUFTSCHMID, 1812) (Coleoptera: Carabidae), *Ocypus olens* (O. MÜLLER, 1764) (Coleoptera: Staphylinidae), *Galeruca tanaceti* (LINNAEUS, 1758) (Coleoptera: Chrysomelidae), *Myrmica sabuleti* MEINERT, 1861 (Hymenoptera: Formicidae), *Tetramorium* cf. *caespitum* (LINNAEUS, 1758) (Hymenoptera: Formicidae), *Tapinoma ambiguum* EMERY, 1925 (Hymenoptera: Formicidae), *Lasius niger* (LINNAEUS, 1758) (Hymenoptera: Formicidae) and *Formica sanguinea* LATREILLE, 1798 (Hymenoptera: Formicidae) and total Isopoda. However, there was a significant increase in numbers of *Kalama tricornis* (SCHRANK, 1801) (Heteroptera: Tingidae), *Lampyris noctiluca* (LINNAEUS, 1767) (Coleoptera: Lampyridae), *Dermestes laniarius* ILLIGER, 1801 (Coleoptera: Dermestidae), *Hahnia nava* (BLACKWALL, 1841) (Araneae: Hahniidae), and in Oribatida, Cicadellidae (Hemiptera) and larvae of Clytrinae (Coleoptera: Chrysomelidae).

Key words: Arthropod assemblage, competition, diversity, Formicidae, invasive species, polygynous ant, predation.

Myrmecol. News 12: 171-181 (online online 25 May 2009)
ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 28 May 2008; revision received 26 January 2009; accepted 28 January 2009

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Introduction

The research of invasive species is an important and imperative challenge of modern ecology (ELTON 1958, MOONEY & DRAKE 1986). Although the vast majority of exotic species either fail or have minor effects on their host commu-

ities (ELTON 1958, SIMBERLOFF 1981, LODGE 1993), a few of them dramatically alter community structure (ELTON 1958, SIMBERLOFF 1981).

Invasive ants form a small and distinct subset of, at least, 150 species of ants introduced into new environments by humans (MCGLYNN 1999). The majority of the introduced ant species remain confined to human-modified habitats and some of these species are often referred to as "tramp" ants because of their human-mediated dispersal and close association with humans (HÖLLDOBLER & WILSON 1990, PASSERA 1994, HOLWAY & al. 2002). A small number of ant species are particularly good invaders (PASSERA 1994, TSUTSUI & SUAREZ 2003), and can have destructive effects on the ecosystems they are introduced to (HOLWAY & al. 2002, SANDERS & al. 2003).

In this study we focus on the invasive garden ant, *Lasius neglectus* VAN LOON, BOOMSMA & ANDRÁSFALVY, 1990. This species has been described from Budapest (Hungary) as a polygynous and supercolonial species (VAN LOON & al. 1990) characteristic of disturbed urban-suburban sites (VAN LOON & al. 1990). Jump dispersal of the ant species may happen by colony budding eventuated by human mediated introduction (ESPADALER & REY 2001, ESPADALER & al. 2007, CREMER & al. 2008, UGELVIG & al. 2008, SCHULTZ & BUSCH 2009). The species was first described in 1990, but it has been found to quickly spread across Europe and Western and Central Asia and by 2008, populations were reported from 109 localities (ESPADALER & al. 2007, ESPADALER & BERNAL 2009, SCHULTZ & BUSCH 2009). *Lasius neglectus* is considered as an invasive pest species (SCHLICK-STEINER & al. 2003, REY & ESPADALER 2004), and shows the main characteristics of the tramp ants (PASSERA 1994). This polygynous species can form enormous supercolonies. In supercolonies, *L. neglectus* can reach higher numbers of workers relative to native ants (TARTALLY 2000), and because of its strong interspecific aggression, can replace native ant species (TARTALLY 2000, CREMER & al. 2006).

Numerous studies have documented the effects of other invasive ants on native ant and arthropod fauna (e.g., RISCH & CARROLL 1982, PORTER & SAVIGNANO 1990, COLE & al. 1992, PASSERA 1994, HUMAN & GORDON 1997, HOLWAY 1998, OLIVERAS & al. 2005), however, only a few studies examined the impact of *L. neglectus* on arthropod assemblages (TARTALLY 2000, TARTALLY & al. 2004, CREMER & al. 2006, DEKONINCK & al. 2007, PARIS 2007). The aim of this study was to compare ant communities and other arthropod fauna in areas where *L. neglectus* was present in high abundance with those found in bordering, similar habitats where this ant species had not reached considerable abundance.

Material and methods

Locality: This study was conducted in the type supercolony of *L. neglectus* in Budatétény, Budapest, Hungary (see VAN LOON & al. 1990). This colony is the largest and probably the oldest in Hungary, its area was approximately 6 km^2 in 2005 (ESPADALER & al. 2007). The climate of Budapest is subcontinental with a rather weak Mediterranean influence. The mean annual temperature is 10.4°C and the annual precipitation is 516 mm (http://met.hu/). The studied area has mostly degraded, weedy vegetation, including a mixture of wooded areas and grassy fields, characterised mainly by ruderal plants and non-native trees (see VAN LOON & al. 1990 for details) and located about 500 m from the nearest houses of the city.

Six sampling sites were established in the study area placed between the motorway M0 and the rail line Budapest – Érd felső; three in the area of the supercolony (supercolony sites: 47° 23' 57" N, 18° 59' 48" E; 47° 23' 57" N, 18° 59' 55" E; 47° 24' 06" N, 19° 00' 38" E) and three found in bordering, similar habitats, where *L. neglectus* had not reached considerable abundance (control sites: 47° 23' 56" N, 18° 59' 28" E; 47° 23' 56" N, 18° 59' 35" E; 47° 23' 57" N, 18° 59' 41" E; see Appendix 1 which is together with Appendices 2 - 4 available as digital supplementary material to this article, at the journal's web pages). All sites were located along a transect crossing the area of the supercolony and all had a similar level of human disturbance. Site 6 was in similar vegetation but farther from the others in the centre of the supercolony (as there was not a long, homogeneous, uninhabited transect found at the borders). Each sampling site had two subunits (five meters from each other at least): one with high (H) and the other with low (L) plant coverage. The subsites with low plant coverage (exclusively herbs) were placed near a dirt road where the grass was regularly mown. An open, and short perennial grassland had arisen caused by the mowing, with a dominance of *Festuca pseudovina* HACK ex WIEB and *Cichorium intybus* L. mixed with the dominant species of roadside weed vegetation, such as *Lolium perenne* L., *Polygonum aviculare* L. and *Plantago lanceolata* L. The high plant density subsites were further from the dirt road and were not mown. Some arboreal plants (*Populus alba* L., *P.* × *euramericana* (DOES), *Salix alba* L., *Robinia pseudoacacia* L., *Sambucus nigra* L., *Cerasus avium* L. and *Maclura pomifera* (RAF.) C.K. SCHNEIDER) were also present there mixed with the herbaceous vegetation.

Sampling methods: Invertebrate sampling was carried out using pitfall traps from 19 March to 28 October 2002. One pitfall trap, covered to exclude small mammals, was placed in both subunits of each sampling site, thus, a total of 12 pitfall traps were set in the study area. Each trap consisted of two plastic cups (200 ml, 7 cm in diameter) buried in the ground and half-filled with 1:1 mixture of water and ethylene glycol. The traps were emptied fortnightly during the seven months and the contents stored in 70% ethyl alcohol. We worked with a relatively low number of traps but through the whole field season. This setup fits to our aim to describe the main effects of *L. neglectus* on the most abundant epigeic arthropods. A higher number of replicates might have yielded more representative samples for some species, but we rather allocated research time to explore a higher number of taxa in this study.

Processing of the collected samples: The collected arthropods were determined to order level and many groups (Opiliones, Araneae, Chilopoda, Isopoda, Dermaptera, Ensifera, Caelifera, Heteroptera, Coleoptera with the exception of most Staphylinidae, and Formicidae) were identified to genus or species by specialists, and counted (see Appendix 4). For the determination and nomenclature of ants we used the works of CZECHOWSKI & al. (2002), SEIFERT (1996) and BOLTON (1995, 1999, 2003). Specimens were labelled and are stored in 70% ethyl alcohol at the first author. Some voucher specimens of rare species were deposited in the collection of the Hungarian Natural History Museum.

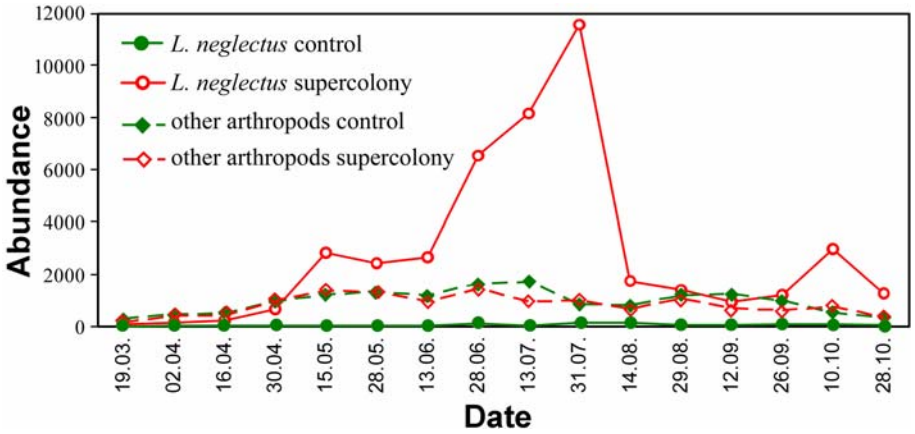

Fig. 1: Seasonal dynamics of *L. neglectus* and all other arthropods in the control and the *L. neglectus* supercolony sites (abundance values on the y axis are the numerical abundance sums across sites).

Tab. 1: The species richness of taxa in the pitfall traps placed on the control and the *L. neglectus* supercolony sites (Welch-test, n.s. = not significant; $^{+}$ = P < 0.1; * = P < 0.05).

Taxa	Control (mean)	Supercolony (mean)	Statistics
All identified species	78.5	78.2	n.s.
Araneae	24.2	24.3	n.s.
Isopoda	4.0	1.7	*
Heteroptera	4.2	6.0	n.s.
Auchenorrhyncha	1.8	3.5	+
Heteroptera + Auchenorrhyncha	6.0	9.5	*
Coleoptera	28.5	33.2	n.s.
Formicidae	9.8	6.3	*

Data analyses: The composition of arthropod assemblages was compared by ordination (nonmetric multidimensional scaling, NMDS). Horn similarity (less sensitive to sample size) was used to compare the species composition and dominance structure of communities, considering the relative abundance of species. The diversity of the samples was compared with the Rényi diversity profile, that characterises the diversity of an assemblage by a family of diversity values, with DIVORD 1.90 PC software package (TÓTHMÉRÉSZ 1995). As a special case it includes the logarithm of the species number ($\alpha = 0$), the Shannon diversity index ($\alpha \rightarrow 1$), the quadratic or Simpson diversity index ($\alpha = 2$), and the logarithm of Berger-Parker diversity ($\alpha \rightarrow \infty$) (TÓTHMÉRÉSZ 1995). The parameter values of the control sites and the supercolony were compared with t-test.

The effect of the supercolony on the abundance data and species richness were analysed by robust two-way ANOVA (Welch's test for the main effect of the supercolony and habitat and Johansen's test for the treatment × habitat interaction) after ln (x + 1) transformation of the abundance data with RobStat statistical package (VARGHA 2008). As the difference in abundance between the high and low plant density subsites is trivial only the results on effect of *L. neglectus* supercolony were presented in the tables of the Results section. In the case of species that were absent from one of the area types two-way stochastic comparison was used instead of robust two-way ANOVA. A correspondence analysis was used to graphically represent the relationships between the analysed species / taxa and the sampling sites.

Results

A total of 68,085 arthropods including 44,595 *L. neglectus* specimens were collected during the period of 2002 (see Appendix 4 for details). *Lasius neglectus* had a superdominant role in the supercolony sites, while its abundance was negligible in the control sites. There was little difference in the total number of arthropods (without *L. neglectus*) between the supercolony (n = 10,826) and control (n = 12,664) sites (Fig. 1).

Lasius neglectus showed activity during the whole sampling period (from 19 March to 28 October) and it was most active in May, June and July with a high peak at the end of July. There was also a smaller peak in the middle of October. Abundance of *L. neglectus* exceeded the total remaining arthropod abundance during most of the sampling period in the supercolony sites, while their number was negligible relative to the total arthropod number in the control sites during the full sampling period (Fig. 1).

Similarity: The analysis of the total invertebrate sample with ordination (NMDS, Horn index), based on orders, showed differences between the compositions of the arthropod assemblages on the control and the supercolony sites (Fig. 2A). This difference remained when *L. neglectus* individuals were excluded from the data (Fig. 2B). The separation was stronger along Axis 1. The composition of the arthropod assemblages was more uniform in the supercolony sites (Figs. 2A, B).

Diversity and species richness: Comparison of the Rényi diversity profiles indicated that the diversity of the total arthropods (all identified species, including *L. neglectus*), and the Coleoptera and Formicidae assemblages was reduced by the ant supercolony (see Appendices 2, 3A, D, E, F). No clear effect of *L. neglectus* was found on the di-

Tab. 2: The mean abundance of ant species from pitfall traps on the control and the *L. neglectus* supercolony sites (n.s. = not significant; $^{+}$ = P < 0.1; * = P < 0.05; ** = P < 0.01; - = no comparison).

Subfamily Species	Control (mean)	Supercolony (mean)	Statistics
Ponerinae			
Ponera coarctata (LATREILLE, 1802)	0.3	0.0	–
Myrmicinae			
Myrmica sabuleti MEINERT, 1861	18.3	0.0	Stochastic comparison*
Myrmica schencki VIERECK, 1903	0.33	1.0	–
Myrmica specioides BONDROIT, 1918	0.3	3.5	–
Solenopsis fugax (LATREILLE, 1798)	10.3	12.0	Welch-test n.s.
Temnothorax crassispinus (KARAVAJEV, 1926)	0.3	71.5	Welch-test n.s.
Myrmecina graminicola (LATREILLE, 1802)	0.0	0.3	–
Tetramorium cf. *caespitum* (LINNAEUS, 1758)	99.0	17.5	Welch-test*
Pyramica baudueri (EMERY, 1875)	0.0	0.2	–
Dolichoderinae			
Tapinoma ambiguum EMERY, 1925	33.0	0.0	Stochastic comparison**
Bothriomyrmex meridionalis (ROGER, 1863)	0.2	0.0	–
Formicinae			
Plagiolepis pygmaea (LATREILLE, 1798)	5.5	0.0	Stochastic comparison^{+}
Camponotus fallax (NYLANDER, 1856)	0.2	0.0	–
Camponotus lateralis (OLIVIER, 1792)	0.2	0.0	–
Lasius fuliginosus (LATREILLE, 1798)	0.5	3.5	–
Lasius neglectus VAN LOON, BOOMSMA & ANDRÁSFALVY, 1990	141.3	7274.7	Welch-test**
Lasius niger (LINNAEUS, 1758)	71.3	0.0	Stochastic comparison**
Lasius (*Chthonolasius*) sp.	0.0	0.5	–
Formica sanguinea LATREILLE, 1798	126.2	0.0	Stochastic comparison*
Formica cunicularia LATREILLE, 1798	4.5	0.0	Stochastic comparison^{+}
Formica rufibarbis FABRICIUS, 1793	55.0	14.2	Welch-test n.s.

versity of total arthropod assemblages without *L. neglectus* and on the diversity of Araneae (see Appendices 2, 3B, C).

The presence of *L. neglectus* caused a significant reduction in species richness of Isopoda (P < 0.05) and Formicidae (P < 0.05), and a significant increase in Hemiptera (excluding Aphididae) (P < 0.05) (Tab. 1).

Effects on ants: A total of 21 native ant species were found nesting in the study area (Tab. 2; see Appendix 4 for taxon authorities of all species recorded). Of the total 22 native ant species collected, *Lasius paralienus* was only represented by two winged females which is no evidence for this species nesting on the sampling sites, for which reason it is not listed in Table 2. From these 21 species found in the studied sites, ten were abundant enough for statistical analysis (more than 25 specimens in the control or supercolony sites). Most of the native epigeic ant species failed to coexist with *L. neglectus*. Six species that were abundant in the control sites were totally absent from the supercolony sites (*Myrmica sabuleti*: P < 0.05, *Tapinoma ambiguum*: P < 0.01, *Plagiolepis pygmaea*: P < 0.1, *Lasius niger*: P < 0.01, *Formica sanguinea*: P < 0.05 and *F. cunicularia*: P < 0.1). Further four species (*Ponera coarctata*, *Bothriomyrmex meridionalis*, *Camponotus fallax*, and *C. lateralis*) were only found in the control sites, but their activity-density was too low for statistical analysis. *Tetramorium* cf. *caespitum* (P < 0.05) was significantly less abundant in the supercolony sites. One epigeic (*Formica rufibarbis*) and two hypogeic (*Solenopsis fugax* and *Temnothorax crassispinus*) species showed no significant difference in abundance between the control and the supercolony sites. Addi-

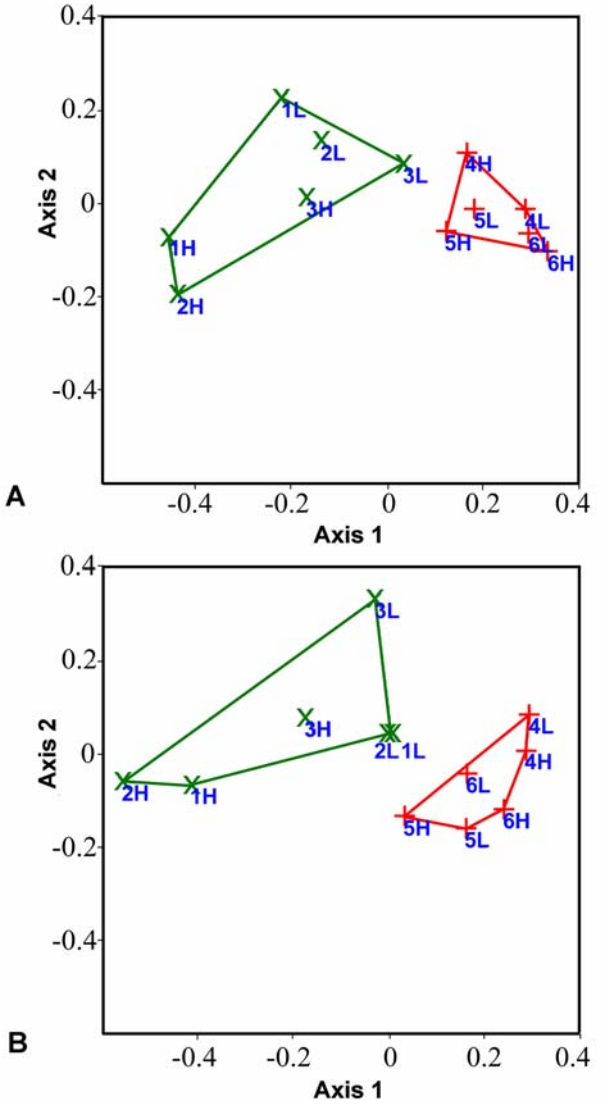

Fig. 2: Ordination (NMDS, Horn similarity) of pitfall trap catches based on (A) the abundance of arthropods grouped at order level, and (B) all identified species, *L. neglectus* excluded (green = control, red = supercolony, H: high plant coverage; L: low plant coverage).

tionally, *Myrmica schencki*, *M. specioides* and *Lasius fuliginosus* were present in the control and the supercolony sites, while *Myrmecina graminicola*, *Pyramica baudueri* and *Chthonolasius* sp. were found only in the supercolony sites. However, the number of the latter species was also too low for statistical analysis.

Effects on non-ant arthropods: A total of five non-ant arthropod species were significantly less abundant in the supercolony sites: *Armadillidium vulgare* (Isopoda: Armadillidiidae): $P < 0.05$, *Trachelipus rathkii* (Isopoda: Trachelipodidae): $P < 0.05$, *Harpalus rubripes* (Coleoptera: Carabidae): $P < 0.05$, *Ocypus olens* (Coleoptera: Staphylinidae): $P < 0.01$, and *Galeruca tanaceti* (Coleoptera: Chrysomelidae): $P < 0.05$. Furthermore, the total abundance of Isopoda was significantly lower in the supercolony sites ($P < 0.01$). In addition, another species, *Drilus concolor* (Coleoptera: Drilidae), had a lower abundance in the supercolony sites, though the difference was only marginally significant ($P < 0.1$). In contrast, four species were significantly more abundant in the supercolony sites. *Kalama tricornis* (Heteroptera: Tingidae): $P < 0.01$, *Dermestes laniarius* (Coleoptera: Dermestidae): $P < 0.01$, *Lampyris noctiluca* (Coleoptera: Lampyridae): $P < 0.01$ and *Hahnia nava* (Araneae: Hahniidae): $P < 0.05$. Furthermore, the total abundance of Oribatida: $P < 0.05$, Cicadellidae: $P < 0.05$ and the larvae of Clytrinae: $P < 0.05$ was also higher in the supercolony sites. Moreover, *Zodarion rubidum* (Araneae: Zodariidae), *Silpha carinata* and *S. obscura* (Coleoptera: Silphidae), *Brachysomus setiger* (Coleoptera: Curculionidae) and Aphididae had a higher abundance in the supercolony sites, though the difference was only marginally significant ($P < 0.1$). There was no difference in the abundance of *Lithobius mutabilis* (Chilopoda: Lithobiidae), *Aulonia albimana* (Araneae: Lycosidae), *Porcellium collicola* (Isopoda: Trachelipodidae), *Dimorphopterus doriae* (Heteroptera: Lygaeidae), *Calathus fuscipes* (Coleoptera: Carabidae), *Drasterius bimaculatus* (Coleoptera: Elateridae), *Crypticus quisquilius* (Coleoptera: Tenebrionidae), and *Lagria hirta* (Coleoptera: Tenebrionidae). Other identified species were not abundant enough to make statistical comparisons (Tab. 3).

Discussion

The abundance of *Lasius neglectus* was extremely high on all of the supercolony sites and strongly exceeded the total number of other arthropods (Fig. 1). Hence, this species had a superdominant role in the supercolony sites in agreement with other studies on invasive ant species (PORTER & SAVIGNANO 1990, HUMAN & GORDON 1997). Although our preliminary studies did not show *L. neglectus* in the control sites, some specimens occurred there later, but only in small numbers (Fig. 1). Thus, it appears that the supercolony was expanding during the study (see also ESPADALER & al. 2007, and Appendix 1).

Lasius neglectus was active during the whole sampling period (from 19 March to 28 October), but not with the same intensity (Fig. 1). The activity was low in the early spring and started rising in May (similarly to the Spanish Seva population, see ESPADALER & BERNAL 2009), possibly due to increasing temperatures, or because of increased food demand for the growing sexual larvae. This rise in activity dropped at the end of July. Accordingly, the strongest effect of the supercolony on other arthropods was seen between May and July, when the activity and the food collecting intensity of *L. neglectus* was the highest.

Although it is known that pitfall trapping might produce unrealistic catching-numbers in the case of some taxa (e.g., for ants see LAEGER & SCHULTZ 2005), it is a widespread standard method well representing the main pattern of abundances, especially in the case of the highly abundant *L. neglectus* (Fig. 1). The invasion of *L. neglectus* in Budatétény caused major changes in the abundance, species richness and diversity of the native ants and other surface active arthropods (Tabs. 1 - 3, Fig. 3; also see Appendices 2, 3A, D - F). In accordance with previous investigations the effect of invasive ants was especially strong on the native ant community, in particular, epigeic ants (PORTER & SAVIGNANO 1990, HUMAN & GORDON 1997, HOLWAY 1998, GÓMEZ & OLIVERAS 2003). Three mechanisms have been proposed to explain the displacement of the native ant fauna caused by ant invasions: exploitative and interference competition (HUMAN & GORDON 1997, HOLWAY 1999), and predation

Tab. 3: The mean abundance of the statistically tested species / taxa (for ants see Tab. 2) from the pitfall traps placed on the control and the *L. neglectus* supercolony sites (n.s. = not significant; $^{+}$ = P < 0.1; * = P < 0.05; ** = P < 0.01).

Taxa	Control (mean)	Supercolony (mean)	Statistics
Chilopoda			
Lithobius mutabilis L. COCK, 1862	6.7	5.0	Welch-test n.s.
Diplopoda			
Julida total	11.7	3.3	Welch-test n.s.
Acari			
Oribatida total	46.0	177.5	Welch-test*
Araneae			
Aulonia albimana (WALCKENAER, 1805)	11.7	4.8	Welch-test n.s.
Zodarion rubidum SIMON, 1914	33.3	55.3	Welch-test^{+}
Hahnia nava (BLACKWALL, 1841)	0.7	5.3	Welch-test*
Isopoda			
Armadillidium vulgare (LATREILLE, 1804)	408.7	22.3	Welch-test*
Porcellium collicola (VERHOEFF, 1907)	99.0	1.7	Welch-test n.s.
Trachelipus rathkii (BRANDT, 1833)	65.2	0.7	Welch-test*
Isopoda total	574.8	25.0	Welch-test**
Collembola			
Collembola total	481.7	506.5	Welch-test n.s.
Heteroptera			
Dimorphopterus doriae (FERRARI, 1874)	13.7	2.3	Welch-test n.s.
Kalama tricornis (SCHRANK, 1801)	0.0	4.7	Stochastic comparison**
Auchenorrhyncha			
Cicadellidae total	4.8	11.5	Welch-test*
Sternorrhyncha			
Aphididae total	10.8	35.5	Welch-test^{+}
Coleoptera			
Calathus fuscipes (GOEZE, 1777)	4.8	5.0	Welch-test n.s.
Harpalus rubripes (DUFTSCHMID, 1812)	20.3	2.0	Welch-test*
Silpha carinata HERBST, 1783	7.3	17.5	Welch-test^{+}
Silpha obscura LINNAEUS, 1758	0.8	17.8	Welch-test^{+}
Silpha spp. larvae	6.0	17.3	Welch-test n.s.
Ocypus olens (O. MÜLLER, 1764)	10.5	1.0	Welch-test**
Drasterius bimaculatus (ROSSI, 1790)	5.0	53.8	Welch-test n.s.
Lampyris noctiluca (LINNAEUS, 1767)	0.0	8.2	Stochastic comparison**
Cantharidae larvae	4.0	12.7	Welch-test n.s.
Dermestes laniarius ILLIGER, 1801	9.5	205.8	Welch-test**
Drilus concolor larvae	6.5	1.8	Welch-test^{+}
Crypticus quisquilius (LINNAEUS, 1761)	9.2	7.0	Welch-test n.s.
Lagria hirta (LINNAEUS, 1758)	3.2	22.7	Welch-test n.s.
Galeruca tanaceti (LINNAEUS, 1758)	13.8	0.7	Welch-test*
Clytrinae larvae	2.5	8.5	Welch-test*
Brachysomus setiger (GYLLENHAL, 1840)	2.7	35.7	Welch-test^{+}

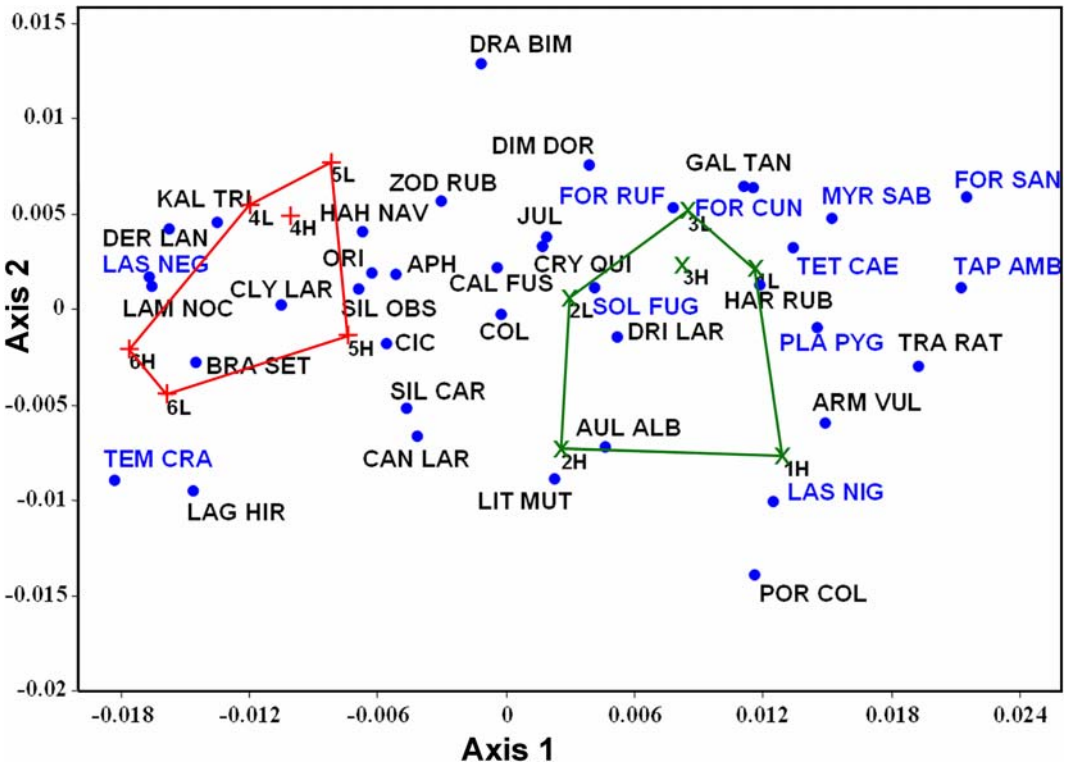

Fig. 3: Correspondence analysis of the analysed species / taxa and the pitfall traps after logarithmic transformation of the data (green = control, red = supercolony, H: high plant coverage; L: low plant coverage, blue capitals = ants, black capitals = non-ant arthropods). Eigenvalues as percentage of variance for axes 1 and 2 were 37.1 and 18.7, respectively. Taxon codes: APH Aphididae, ARM VUL *Armadillidium vulgare*, AUL ALB *Aulonia albimana*, BRA SET *Brachysomus setiger*, CAL FUS *Calathus fuscipes*, CAN LAR Cantharidae larvae, CIC Cicadellidae, CLY LAR Clytrinae larvae, COL Collembola, CRY QUI *Crypticus quisquilius*, DER LAN *Dermestes laniarius*, DIM DOR *Dimorphopterus doriae*, DRA BIM *Drasterius bimaculatus*, DRI LAR *Drilus concolor* larvae, FOR CUN *Formica cunicularia*, FOR RUF *Formica rufibarbis*, FOR SAN *Formica sanguinea*, GAL TAN *Galeruca tanaceti*, HAH NAV *Hahnia nava*, HAR RUB *Harpalus rubripes*, JUL Julida, KAL *Kalama tricornis*, LAG HIR *Lagria hirta*, LAM NOC *Lampyris noctiluca*, LAS NEG *Lasius neglectus*, LAS NIG *Lasius niger*, LIT MUT *Lithobius mutabilis*, MYR SAB *Myrmica sabuleti*, ORI Oribatida, PLA PYG *Plagiolepis pygmaea*, POR COL *Porcellium collicola*, SIL CAR *Silpha carinata*, SIL OBS *Silpha obscura*, SOL FUG *Solenopsis fugax*, TAP AMB *Tapinoma ambiguum*, TEM CRA *Temnothorax crassispinus*, TET CAE *Tetramorium* cf. *caespitum*, TRA RAT *Trachelipus rathkii*, ZOD RUB *Zodarion rubidum*.

(ZEE & HOLWAY 2006). Highly aggressive interactions have been observed between *L. neglectus* and many other ant species both in laboratory (CREMER & al. 2006) and field experiments (TARTALLY 2000).

Only workers of ten native ant species were collected in the supercolony sites in contrast to the 17 species collected in the control sites (Tab. 2). These results confirm that the role of *L. neglectus* in the organization of local ant fauna is very strong (Tabs. 1, 2; also see Appendices 2, 3E, F). This is interesting because some researchers argue that declines in native ant diversity result more from human disturbance than from displacement by invasive ants (e.g., KING & TSCHINKEL 2006). The present study argues for a direct effect of *L. neglectus* on other ant species. Six epigeic ants, existing in the control sites, were fully absent from the supercolony sites. It should be emphasized that *Tetramorium* cf. *caespitum* was relatively common in the supercolony sites but significantly rarer than in the control sites. However, six other ant species were also found in the supercolony sites but only in a very low abundance (Tab. 2). Abundance values of three species (*Solenopsis fugax*, *Temnothorax crassispinus* and *Formica rufibarbis*) did not show significant differences between the control and supercolony sites.

Solenopsis fugax is a microendogeic, small sized species, feeding almost always under the ground surface (GALLÉ 1972, 1994). This species is often associated with larger *Formica* and *Lasius* species preying on their brood (COLLINGWOOD 1979). Colonies of *S. fugax* were present even within the nest of *L. neglectus* (C. Nagy & al., unpubl.), leading to the assumption that there is no serious negative effect on this species.

The activity-density of *T. crassispinus* was fairly high in the supercolony sites. This species has small colonies

nesting in tree branches, dry plant particles, crops and rolled leafs (STRÄTZ & HEINZE 2004) hence its microhabitat probably does not overlap with *L. neglectus*. Other studies have shown that a similar species, *Temnothorax andrei* (EMERY, 1895), is able to coexist with the Argentine ant (HOLWAY 1998, SUAREZ & al. 1998, SUAREZ & CASE 2003), and a Mediterranean small sized cryptic species, *Temnothorax lichtensteini* (BONDROIT, 1918), is capable of coexisting with *L. neglectus*, because it nests under bark. It is thought that by having a low abundance these ants are less likely to have an encounter with *L. neglectus* (see PARIS 2007). The same situation may be true for *T. crassispinus*.

Formica rufibarbis is a subordinate opportunistic species. Its ability to coexist with *L. neglectus* may, in part, be due to its activity at a different time of the day. It also has a rapid motility which may enable it to escape from the attack of *L. neglectus* workers (TARTALLY 2000). Although this species often coexists with the dominant *Lasius* species in Hungary (GALLÉ 1994), founding new colonies in a *L. neglectus* supercolony area is probably difficult. We observed that recently mated *F. rufibarbis* queens were attacked by *L. neglectus* workers (C. Nagy & al., unpubl.). Strikingly, the ecologically very similar (GALLÉ 1994) *Formica cunicularia* was completely absent from the supercolony sites.

The presence of a *L. neglectus* supercolony also reduces (Tab. 3) the abundance of some non-ant species (*Armadillidium vulgare*, *Trachelipus rathkii*, *Harpalus rubripes*, *Ocypus olens* and *Galeruca tanaceti*) or arthropod groups (Isopoda; except for the myrmecophilous invader, *Platyarthrus schoblii* BUDDE-LUND, 1885 and its native relative, *P. hoffmannseggii*, see TARTALLY & al. 2004, HORNUNG & al. 2005). However, other taxa can exist or thrive in the presence of the supercolonies (*Hahnia nava*, *Kalama tricornis*, *Lampyris noctiluca*, *Dermestes laniarius,* Oribatida, Cicadellidae, Clytrinae larvae), maybe through processes such as mutualism, commensalism, parasitism, predation or scavenging.

Decreases in population size may be attributed to several factors: predation or competition by the invasive ants and dependence upon organisms displaced by them (HUMAN & GORDON 1997). Slow moving invertebrates may be more susceptible to direct predation. Two Isopoda species (*A. vulgare*, *T. rathkii*) were significantly less represented in the supercolony sites (Tab. 3). One explanation for this pattern could be that the juveniles of Isopoda species are preyed upon by *L. neglectus*. The results of previous studies on the effect of invasive ants on Isopoda species are fairly conflicting. For example, *A. vulgare* was negatively affected by *Solenopsis invicta* BUREN, 1972 (PORTER & SAVIGNANO 1990), but their abundance increased in the presence of *Linepithema humile* (MAYR, 1868) (HUMAN & GORDON 1997). Abundance of another Isopoda species (*Porcellio laevis* LATREILLE, 1804) was also increased in the presence of *L. humile* on the Hawaiian Islands (COLE & al. 1992). Our results suggest a strong negative effect of the *L. neglectus* supercolony on the Isopoda assemblages. *Armadillidium vulgare* is a cosmopolitan species (SCHMALFUSS 2003) able to achieve some protection by rolling into a ball and thus decreasing exposure of more vulnerable parts of the body which enables them to exist in the smaller *L. neglectus* colonies. The other two Isopoda species cannot roll into a ball as a defensive strategy, so they are unable to protect themselves against *L. neglectus* attack. *Lasius neglectus* has been observed preying on Trachelipodidae species in dry pitfall traps (C. Nagy & al., unpubl.).

Harpalus rubripes (Coleoptera: Carabidae), *O. olens* (Coleoptera: Staphylinidae) and *G. tanaceti* (Coleoptera: Chrysomelidae) were less abundant in the supercolony sites (Tab. 3). The results of other studies on invasive ants and Carabidae are not in agreement. Some studies showed negative effects (COLE & al. 1992, BOLGER & al. 2000), others showed positive effects (HUMAN & GORDON 1997), while some found carabid beetles unaffected by the ants (HOLWAY 1998). This study showed a negative effect on *H. rubripes* and the reason could be predation by *L. neglectus* on the eggs and larvae of this carabid species. Previous reports have shown that Argentine ants prey upon arthropod eggs (DRIESTADT & al. 1986, WAY & al. 1992). It is also possible that, as an indirect effect of *L. neglectus*, there is a decrease in prey availability for this carabid species on these sites. The situation can be similar in the case of *O. olens* too. *Galeruca tanaceti* is a polyphagous, ground surface active chrysomelid species (SÁRINGER 1990). Previous studies have suggested that invasive ants can reduce the abundance of some chrysomelid species (BOLGER & al. 2000, HARVEY & EUBANKS 2004). HARVEY & EUBANKS (2004) found two species from the subfamily Galerucinae negatively affected by *S. invicta*. Our results confirm this although reasons for this are not clear. *Lasius neglectus* may prey upon the young larvae of *G. tanaceti*, however the poison-content of *Galeruca* species (SELMAN 1988) would suggest that this is not the case, unless *L. neglectus* is resistant to the poison or only receives a sublethal dose.

Explanation for the increase in the population size of some organisms in areas with invasive ants are numerous and include avoidance, reduction of other predators, physical protection (e.g., exoskeletons, chemical defences) and non-overlapping habitats (PORTER & SAVIGNANO 1990, COLE & al. 1992, HUMAN & GORDON 1997). Some researchers have suggested that numbers of scavengers could increase in the presence of invasive ants because significantly larger ant populations lead to higher numbers of dead ants and prey remains (PORTER & SAVIGNANO 1990, COLE & al. 1992, HUMAN & GORDON 1997). PORTER & SAVIGNANO (1990) found two scavenger species, a brachypterous roach (Blattellidae) and a ground cricket (Gryllidae: *Neonemobius mormonius* (SCUDDER, 1896)), increasing in abundance in the supercolony of *S. invicta*. Perhaps these two species fed on dead fire ants that commonly accumulated in large numbers in the infested area (PORTER & SAVIGNANO 1990). COLE & al. (1992) found an increased abundance of the adventive coleopteran species in the area of a *L. humile* supercolony. These species were mostly scavengers and one of them was a *Dermestes* species. In our study one scavenger species (*D. laniarius*, Coleoptera: Dermestidae) and a scavenger group (Oribatida) were highly abundant on *L. neglectus* invaded areas (Tab. 3). After *L. neglectus*, *D. laniarius* had the second highest abundance from the identified species on the supercolony sites. Reasons for this include: (1) Larvae of *Dermestes* species are scavengers feeding on dead insects, chitin remains (MERKL 2003); (2) larvae of this species have long setae (MERKL 2003) which may protect them against *L. neglectus*. Hence, the increase of this species may be the result of a high amount of skeleton remains accumulated near *L. neglec-*

tus nests. Larvae of *D. laniarius* feeding on chitin particles were observed in the vicinity of *L. neglectus* nest entrances (C. Nagy & al., unpubl.).

Oribatida was the other scavenger group found in significantly higher numbers in the supercolony sites. Previous studies were not found to support this phenomenon, but members of this order have small sized and highly sclerotized bodies which might protect them against *L. neglectus*.

Previous studies have found negative (HAINES & HAINES 1978, LUBIN 1984, COLE & al. 1992, HUMAN & GORDON 1997), neutral (PORTER & SAVIGNANO 1990, PARIS 2007) or positive (BOLGER & al. 2000) effects of invasive ants on spiders. Our study found *Hahnia nava* in significantly higher numbers in the supercolony sites and also more *Zodarion rubidum* were collected in the supercolony sites, though the difference in the latter was not significant ($P < 0.1$) (Tab. 3). Evidence for predation of *H. nava* on ants has not been reported to date, but *Z. rubidum* is a specialist ant-feeder (PEKÁR 2004). PEKÁR (2004) showed that *Z. rubidum* fed on *T.* cf. *caespitum* and *L. platythorax* SEIFERT, 1991 ants. *Lasius neglectus* is of similar size as those ants and thus may also be preyed on by *Z. rubidum*. It is already known that ant invasion can positively affect the abundance of a myrmecophagic spider (TOUYAMA & al. 2008).

Kalama tricornis (SCHRANK, 1801) (Heteroptera: Tingidae) had significantly higher abundance in the supercolony sites (Tab. 3) which is not surprising given the earlier observations on this species from ant colonies (e.g., DONISTHORPE 1902). There are some reports also on other Heteroptera families: COLE & al. (1992), EUBANKS (2001) and EUBANKS & al. (2002) showed a negative effect, while RISCH & CARROLL (1982) and PORTER & SAVIGNANO (1990) found no effect of invasive ants on heteropterans.

The abundance of the family Cicadellidae was significantly higher in the supercolony sites (Tab. 3). Cicadellidae produce honeydew and can form mutualistic interactions with ants (STEINER & al. 2004). STEINER & al. (2004) found a *Lasius* species (*L. alienus*) visiting a cicadellid leafhopper species. It is possible, although not observed in this study, that there may be a similar relationship with *L. neglectus*.

Significantly higher numbers of Clytrinae larvae (Coleoptera: Chrysomelidae) were found in the supercolony sites (Tab. 3). These larvae develop in ant nests as commensalists or feeding on ant eggs and larvae (SELMAN 1988). ESPADALER & BERNAL (2009) also found few larvae of a Clytrinae species (*Clytra laeviuscula*) inside the nest of *L. neglectus*.

Lampyris noctiluca (Coleoptera: Lampyridae) was also associated with the supercolony sites (Tab. 3). This carnivorous species feeds mostly on snails and insect larvae (KASZAB 1955). The reason for their higher number in the presence of *L. neglectus* is not clear. RISCH & CARROLL (1982) found more Lampyridae specimens in the presence of *Solenopsis geminata* (FABRICIUS, 1804), but this difference was not significant. SIVINSKI & al. (1998) found a Lampyridae species (*Pleotomodes needhami* GREEN, 1948) living in the nest of three ant species, and noticed some other myrmecophile firefly species too. However, predation by the firefly specimens on ant brood was not observed (SIVINSKI & al. 1998). There is no evidence of similar myrmecophily of *L. noctiluca*, but this interaction needs further research.

In some other species (Tab. 3) we found only marginally significant differences between the supercolony and control sites. Further targeted investigations with higher sampling effort may show clearer effects in the case of these and other species, too.

In summary, this study shows that *L. neglectus* has a strong effect on the arthropod fauna. Due to the important and strong role of this invasive species in the organization of arthropod assemblages, further ecological studies are necessary on its influence on native communities. This species can represent a serious threat to the biodiversity of local ecosystems, emphasising the need for monitoring and biocontrol of *L. neglectus*.

Acknowledgements

We thank Erzsébet Hornung, László Dányi and Gábor Dániel Lengyel for their help in invertebrate identification (see Appendix 4) and László Somay for botanical survey. Michelle Fountain gave advice and suggested useful corrections on an earlier version of the manuscript. Roland Schultz, an anonymous referee and the editors provided very constructive comments.

Zusammenfassung

Invasive Ameisenarten stellen eine ernste Bedrohung vieler ökologischer Gemeinschaften dar, indem sie Abnahmen von Abundanz, Artenreichtum und Diversitätsindizes nativer Ameisen und anderer Arthropoden bedingen. Die Ameise *Lasius neglectus* VAN LOON, BOOMSMA & ANDRÁSFALVY, 1990, auch "invasive garden ant" genannt, ist eine invasive Art, die dichte Superkolonien bildet. Wir haben die ökologischen Auswirkungen der Typus-Superkolonie dieser Art auf andere Ameisen und oberflächenaktive Arthropoden in Budatétény, Budapest, Ungarn, untersucht. Abundanzen, Artenreichtum und Diversitätsindizes von Arthropoden wurden auf der Basis von Barberfallenfängen geschätzt.

Die *L. neglectus*-Superkolonie hat die Zusammensetzung der Arthropodengemeinschaft drastisch verändert. Für Arthropoden insgesamt, für Coleoptera und für andere Formicidae waren die Diversitätsindizes in den Bereichen der *L. neglectus*-Superkolonie niedriger als in den Kontrollbereichen außerhalb dieser. Die Anwesenheit von *L. neglectus* verursachte eine signifikante Abnahme des Artenreichtums von Isopoda und anderen Formicidae, aber eine signifikante Zunahme der Hemiptera.

Lasius neglectus hatte einen signifikant negativen Effekt auf die Abundanz der Arthropodenarten *Armadillidium vulgare* (LATREILLE, 1804) (Isopoda: Armadillidiidae), *Trachelipus rathkii* (BRANDT, 1833) (Isopoda: Trachelipodidae), *Harpalus rubripes* (DUFTSCHMID, 1812) (Coleoptera: Carabidae), *Ocypus olens* (O. MÜLLER, 1764) (Coleoptera: Staphylinidae), *Galeruca tanaceti* (LINNAEUS, 1758) (Coleoptera: Chrysomelidae), *Myrmica sabuleti* MEINERT, 1861 (Hymenoptera: Formicidae), *Tetramorium* cf. *caespitum* (LINNAEUS, 1758) (Hymenoptera: Formicidae), *Tapinoma ambiguum* EMERY, 1925 (Hymenoptera: Formicidae), *Lasius niger* (LINNAEUS, 1758) (Hymenoptera: Formicidae) und *Formica sanguinea* LATREILLE, 1798 (Hymenoptera: Formicidae) sowie auf die Isopoda insgesamt. Im Gegensatz dazu zeigte sich eine signifikante Abundanzzunahme bei *Kalama tricornis* (SCHRANK, 1801) (Heteroptera: Tingidae), *Lampyris noctiluca* (LINNAEUS, 1767) (Coleoptera: Lampyridae), *Dermestes laniarius* ILLIGER, 1801 (Coleo-

ptera: Dermestidae), *Hahnia nava* (BLACKWALL, 1841) (Araneae: Hahniidae) sowie bei den Oribatida, Cicadellidae (Hemiptera) und Larven von Clytrinae (Coleoptera: Chrysomelidae).

References

BOLGER, D.T., SUAREZ, A.V., CROOKS, K.R., MORRISON, S.A. & CASE, T.J. 2000: Arthropods in urban habitat fragments in southern California: Area, age, and edge effects. – Ecological Applications 10: 1230-1248.

BOLTON, B. 1995: A new general catalogue of the ants of the world. – The Belknap Press of Harvard University Press, Cambridge, MA, 504 pp.

BOLTON, B. 1999: The ant genera of the tribe Dacetonini (Hymenoptera: Formicidae). – Journal of Natural History 33: 1639-1689.

BOLTON, B. 2003: Synopsis and classification of Formicidae. – Memoirs of the American Entomological Institute 71: 1-370.

COLE, F.R., MEDEIROS, A.C., LOOPE, L.L. & ZUEHLKE, W.W. 1992: Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. – Ecology 73: 1313-1322.

COLLINGWOOD, C.A. 1979: The Formicidae (Hymenoptera) of Fennoscandia and Denmark. – Fauna Entomologica Scandinavica 8: 1-174.

CREMER, S., UGELVIG, L.V., DRIJFHOUT, F.P., SCHLICK-STEINER, B.C., STEINER, F.M., SEIFERT, B., HUGHES, D.P., SCHULZ, A., PETERSEN, K.S., KONRAD, H., STAUFFER, C., KIRAN, K., ESPADALER, X., D'ETTORRE, P., AKTAÇ, N., EILENBERG, J., JONES, G.R., NASH, D.R., PEDERSEN, J.S. & BOOMSMA, J.J. 2008: The evolution of invasiveness in garden ants. – Public Library of Science ONE 3: e3838.

CREMER, S., UGELVIG, L.V., LOMMEN, S.T.E., PETERSEN, K.S. & PEDERSEN, J.S. 2006: Attack of the invasive garden ant: aggression behaviour of *Lasius neglectus* (Hymenoptera: Formicidae) against native *Lasius* species in Spain. – Myrmecologische Nachrichten 9: 13-19.

CZECHOWSKI, W., RADCHENKO, A. & CZECHOWSKA, W. 2002: The ants (Hymenoptera, Formicidae) of Poland. – Muzeum i Instytut Zoologii PAN, Warszawa, 200 pp.

DEKONINCK, W., LOCK, K. & JANSSENS, F. 2007: Acceptance of two native myrmecophilous species, *Platyarthrus hoffmannseggii* (Isopoda: Oniscidea) and *Cyphoderus albinus* (Collembola: Cyphoderidae) by the introduced invasive garden ant *Lasius neglectus* (Hymenoptera: Formicidae) in Belgium. – European Journal of Entomology 104: 159-161.

DONISTHORPE, H.J.K. 1902: Notes on the British myrmecophilous fauna (excluding Coleoptera). – Entomologist's Record 14: 37-40.

DREISTADT, S.H., HAGEN, K.S. & DAHLSTEN, D.L. 1986: Predation by *Iridomyrmex humilis* (Hym.: Formicidae) on eggs of *Chrysoperla carnea* (Neu.: Chrysopidae) released for inundative control of *Illinoia liriodendri* (Hom.: Aphididae) infesting *Liriodendron tulipifera*. – Entomophaga 31: 397-400.

ELTON, C.S. 1958: The ecology of invasions by animals and plants. – Methuen, London, 181 pp.

ESPADALER, X. & BERNAL, V. 2009: *Lasius neglectus*, a polygynous, sometimes invasive, ant. – <http://www.creaf.uab.es/xeg/Lasius/Ingles/index.htm>, retrieved on 13 January 2009.

ESPADALER, X. & REY, S. 2001: Biological constraints and colony founding in the polygynous invasive ant *Lasius neglectus* (Hymenoptera, Formicidae). – Insectes Sociaux 48: 159-164.

ESPADALER, X., TARTALLY, A., SCHULTZ, R., SEIFERT, B. & NAGY, C. 2007: Regional trends and preliminary results on the local expansion rate in the invasive garden ant, *Lasius neglectus* (Hymenoptera, Formicidae). – Insectes Sociaux 54: 293-301.

EUBANKS, M.D. 2001: Estimates of the direct and indirect effects of red imported fire ants on biological control. – Biological Control 21: 35-43.

EUBANKS, M.D., BLACKWELL, S.A., PARRISH, C.J., DELAMAR, Z.D. & HULL-SANDERS, H. 2002: Intraguild predation of beneficial arthropods by red imported fire ants in cotton. – Environmental Entomology 31: 1168-1174.

GALLÉ, L. 1972: Formicidae populations of the ecosystems in the environs of Tiszafüred. – Tiscia 7: 59-68.

GALLÉ, L. 1994: Formicoidea közösségek szerveződése. – Academic Doctoral Thesis, University of Szeged, Szeged, 125 pp.

GÓMEZ, C. & OLIVERAS, J. 2003: Can the Argentine ant (*Linepithema humile* MAYR) replace native ants in myrmecochory? – Acta Oecologica 24: 47-53.

HAINES, I.H. & HAINES, J.B. 1978: Colony structure, seasonality and food requirements of the crazy ant, *Anoplolepis longipes* (JERD.), in the Seychelles. – Ecological Entomology 3: 109-118.

HARVEY, C.T. & EUBANKS, M.D. 2004: Effect of habitat complexity on biological control by the red imported fire ant (Hymenoptera: Formicidae) in collards. – Biological Control 29: 348-358.

HOLWAY, D.A. 1998: Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. – Oecologia 116: 252-258.

HOLWAY, D.A. 1999: Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. – Ecology 80: 238-251.

HOLWAY, D.A., LACH, L., SUAREZ, A.V., TSUTSUI, N.D. & CASE, T.J. 2002: The causes and consequences of ant invasions. – Annual Review of Ecology and Systematics 33: 181-233.

HÖLLDOBLER, B. & WILSON, E.O. 1990: The ants. – The Belknap Press of Harvard University Press, Cambridge, MA, 732 pp.

HORNUNG, E., VILISICS, F. & TARTALLY, A. 2005: Occurrence of *Platyarthrus schoblii* (Isopoda, Oniscidea) and its ant hosts in Hungary. – European Journal of Soil Biology 41: 129-133.

HUMAN, K.G. & GORDON, D.M. 1997: Effects of Argentine ants on invertebrate biodiversity in northern California. – Conservation Biology 11: 1242-1248.

KASZAB, Z. 1955: Különböző csápú bogarak-Diversicornia I. Lágytestű bogarak-Malacodermata. – Magyarország állatvilága 8: 1-144.

KING, J.R. & TSCHINKEL, W.R. 2006: Experimental evidence that the introduced fire ant, *Solenopsis invicta*, does not competitively suppress co-occurring ants in a disturbed habitat. – Journal of Animal Ecology 75: 1370-1378.

LAEGER, T. & SCHULTZ, R. 2005: Ameisen als Beifänge in Bodenfallen – wie genau spiegeln sie reale Abundanzverhältnisse wider? – Myrmecologische Nachrichten 7: 17-24.

LODGE, D.M. 1993: Biological invasions: lessons for ecology. – Trends in Ecology and Evolution 8: 133-137.

LUBIN, Y.D. 1984: Changes in the native fauna of the Galapagos Islands following invasion by the little red fire ant, *Wasmannia auropunctata*. – Biological Journal of the Linnean Society 21: 229-242.

MCGLYNN, T.P. 1999: Non-native ants are smaller than related native ants. – American Naturalist 154: 690-699.

MERKL, O. 2003: Bogarak. – Kossuth Kiadó, Budapest, 112 pp.

MOONEY, H.A. & DRAKE, J.A. 1986: Ecology of biological invasions of North America and Hawaii. – Springer-Verlag, New York, 321 pp.

OLIVERAS, J., BAS, J.M., CASELLAS, D. & GOMEZ, C. 2005: Numerical dominance of the Argentine ant vs native ants and consequences on soil resource searching in Mediterranean cork-oak forests (Hymenoptera: Formicidae). – Sociobiology 45: 643-658.

PARIS, C.I. 2007: Above-belowground effects of the invasive ant *Lasius neglectus* in an urban holm oak forest. – PhD thesis, Autonomous University of Barcelona, Bellaterra, 150 pp.

PASSERA, L. 1994: Characteristics of tramp species. In: WILLIAMS, D.F. (Ed.). Exotic ants: biology, impact and control of introduced species. – Westview Press, Boulder, CO, pp. 23-43.

PEKÁR, S. 2004: Predatory behavior of two European ant-eating spiders (Araneae, Zodariidae). – Journal of Arachnology 32: 31-41.

PORTER S.D. & SAVIGNANO, D.A. 1990: Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. – Ecology 71: 2095-2106.

REY, S. & ESPADALER, X. 2004: Area-wide management of the invasive garden ant *Lasius neglectus* (Hymenoptera: Formicidae) in Northeast Spain. – Journal of Agricultural and Urban Entomology 21: 99-112.

RISCH, S.J. & CARROLL, C.R. 1982: Effect of a keystone predaceous ant, *Solenopsis geminata*, on arthropods in a tropical ecosystem. – Ecology 63: 1979-1983.

SANDERS, N.J., GOTELLI, N.J., HELLER, N.E. & GORDON, D.M. 2003: Community disassembly by an invasive species. – Proceedings of the National Academy of Sciences of the United States of America 100: 2474-2477.

SÁRINGER, G. 1990: Levélbogarak (Chrysomelidae). In: JERMY, T. & BALÁZS, K. (Eds.): A növényvédelmi állattan kézikönyve. – Akadémiai Kiadó, Budapest, pp. 234-321.

SCHLICK-STEINER, B.C., STEINER, F.M., SCHÖDL, S. & SEIFERT, B. 2003: *Lasius austriacus* sp.n., a Central European ant related to the invasive species *Lasius neglectus*. – Sociobiology 41: 725-736.

SCHMALFUSS, H. 2003: World catalog of terrestrial isopods (Isopoda: Oniscidea). – Stuttgarter Beiträge zur Naturkunde Serie A (Biologie) 654: 1-341.

SCHULTZ, R. & BUSCH, T. 2009: The northernmost record of the invasive garden ant, *Lasius neglectus* (Hymenoptera: Formicidae). – Myrmecological News 12: 183-186.

SEIFERT, B. 1996: Ameisen, beobachten, bestimmen. – Naturbuch Verlag, Augsburg, 352 pp.

SELMAN, B.J. 1988: Chrysomelids and ants. In: JOLIVET, P., PETITPIERRE, E. & HSIAO, T.H. (Eds.): Biology of Chrysomelidae. – Kluwer Academic Publishers, Dordrecht, pp. 463-473.

SIMBERLOFF, D. 1981: Community effects of introduced species. In: NITECKI, N. (Ed.): Biotic crises in ecological and evolutionary times. – Academic Press, New York, pp. 53-81.

SIVINSKI, J.M., LLOYD, J.E., BESHERS, S.N., DAVIS, L.R., SIVINSKI, R.G., WING, S.R., SULLIVAN, R.T., CUSHING, P.E. & PETERSSON, E. 1998: A natural history of *Pleotomodes needhami* GREEN (Coleoptera: Lampyridae): a firefly symbiont of ants. – The Coleopterists Bulletin 52: 23-30.

STEINER, F.M., SCHLICK-STEINER, B.C., HOLZINGER, W., KOMPOSCH, C., PAZOUTOVA, S., SANETRA, M. & CHRISTIAN, E. 2004: A new relationship between ants and a leafhopper (Hymenoptera: Formicidae; Hemiptera: Cicadellidae). – European Journal of Entomology 101: 689-692.

STRÄTZ, M. & HEINZE, J. 2004: Colony structure and sex allocation ratios in the ant *Temnothorax crassispinus*. – Insectes Sociaux 51: 372-377.

SUAREZ, A.V., BOLGER, D.T. & CASE, T.J. 1998: Effects of fragmentation and invasion on native ant communities in coastal southern California. – Ecology 79: 2041-2056.

SUAREZ, A.V. & CASE, T.J. 2003: The ecological consequences of a fragmentation mediated invasion: the argentine ant, *Linepithema humile*, in Southern California. In: BRADSHAW, G.A. & MARQUET, P. (Eds.): How landscapes change: human disturbance and ecosystem disruptions in the Americas. Ecological Studies 162. – Springer-Verlag, Berlin, pp. 161-180.

TARTALLY, A. 2000: Notes on the coexistence of the supercolonial *Lasius neglectus* VAN LOON, BOOMSMA et ANDRÁSFALVY 1990 (Hymenoptera: Formicidae) with other ant species. – Tiscia 32: 43-46.

TARTALLY, A., HORNUNG, E. & ESPADALER, X. 2004: The joint introduction of *Platyarthrus schoblii* (Isopoda: Oniscidea) and *Lasius neglectus* (Hymenoptera: Formicidae) into Hungary. – Myrmecologische Nachrichten 6: 61-66.

TÓTHMÉRÉSZ, B. 1995: Comparison of different methods of diversity ordering. – Journal of Vegetation Science 6: 283-290.

TOUYAMA, Y., IHARA, Y. & ITO, F. 2008: Argentine ant infestation affects the abundance of the native myrmecophagic jumping spider *Siler cupreus* SIMON in Japan. – Insectes Sociaux 55: 144-146.

TSUTSUI, N.D. & SUAREZ, A.V. 2003: The colony structure and population biology of invasive ants. – Conservation Biology 17: 48-58.

UGELVIG, L.V., DRIJFHOUT, F.P., KRONAUER, D.J.C., BOOMSMA, J.J., PEDERSEN, J.S. & CREMER, S. 2008: The introduction history of invasive garden ants in Europe: integrating genetic, chemical and behavioural approaches. – BMC Biology 6: 11.

VAN LOON, A.J., BOOMSMA, J.J. & ANDRÁSFALVY, A. 1990: A new polygynous *Lasius* species (Hymenoptera: Formicidae) from central Europe. I. Description and general biology. – Insectes Sociaux 37: 348-362.

VARGHA, A. 2008: The statistical menu system of ROPSTAT. – <http://www.ropstat.com>, retrieved on 9 December 2008.

WAY, M.J., CAMMELL, M.E. & PAIVA, M.R. 1992: Studies on egg predation by ants (Hymenoptera: Formicidae) especially on the eucalyptus borer *Phoracantha semipunctata* (Coleoptera: Cerambycidae) in Portugal. – Bulletin of Entomological Research 82: 425-432.

ZEE, J. & HOLWAY, D. 2006: Nest raiding by the invasive Argentine ant on colonies of the harvester ant, *Pogonomyrmex subnitidus*. – Insectes Sociaux 53: 161-167.